Macronematine caddisflies of the genus *Amphipsyche* (Trichoptera: Hydropsychidae)

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Synopsis

In this revision of the genus *Amphipsyche* McLachlan 22 species are recognized, of which two are described as new. One new generic and ten new specific synonyms are established, and one species is transferred to *Amphipsyche* from *Protomacronema* Ulmer. Eight lectotypes are designated. Keys are given to the Old World genera of the tribe Macronematini and to the species of *Amphipsyche*. The classification of the species is based on a cladistic analysis, and some of the evolutionary and zoogeographical implications of the analysis are discussed.

Introduction

Amphipsyche McLachlan is an Old World genus of caddisflies having netspinning larvae that are frequently found in fast freshwater streams throughout the Afrotropical and Oriental regions. Some species have figured prominently in recent freshwater pollution and impoundment studies, and at least one species is a predator on larvae of *Simulium* Latreille (Diptera).

Many of the recent ecological studies on tropical freshwater habitats are the result of the pressing need for knowledge of the effects of man's activities, the most obvious of which is direct pollution of the water by chemical or other agents. Although most Trichoptera are very sensitive to such pollutants and tend to disappear even at low levels of contamination, there is a selective response shown by different species of caddis. Resh & Unzicker (1975) have stressed that it is important to be able to identify the organisms at the specific level for this kind of study. Another important influence of man is the damming of rivers for hydroelectric or irrigation schemes. Although the ecology of such impounded water is usually studied, the effects on the regulated river itself are less well known and the few existing reports suggest that the natural watercourse may be altered for a considerable distance downstream of the impoundment. The release of

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water rich in zooplankton from these dams leads to large populations of filter-feeding organisms such as Hydropsychidae, and among these *Amphipsyche* has often been reported as reaching pest proportions. However, it should be noted that the discharge of cold hypolimnial water from dams can suppress the populations of such organisms immediately below the impoundment (Stanford & Ward, 1981). *Simulium*, another filter-feeder, can also occur in large numbers in such habitats, and various insecticides such as DDT have been used to control populations of the *S. damnosum* complex, the vector of onchocerciasis. The effects of these control agents on non-target organisms is always monitored, and because *Amphipsyche* occurs at similar sites it has often figured prominently in such studies (Corbet, 1958*a*; Statzner, 1981). *Amphipsyche scottae* is also known to be a predator of *Simulium* (Chutter, 1968).

The identification of the organisms collected in all such freshwater studies, especially in the tropics, is always a major problem. Scott (1975) stated that the larval stages of less than 15 per cent of the African Trichoptera were known, and the corresponding figure for Asia must be considerably lower. Such identification relies on the correct association of larvae and adults, which often depends on long-term collecting programmes and rearing in the field; equally important is the provision of reliable keys for the identification of adults. The netspinning larvae of the Hydropsychidae are often one of the most abundant groups of macro-invertebrates in running water, and as part of a continuing study of the subfamily Macronematinae this paper deals with the adults of the genus *Amphipsyche*, in the tribe Macronematini. The species in this genus are superficially very similar to each other, and they also resemble species of *Aethaloptera* Brauer, in the Polymorphanisini (Barnard, 1980); I have frequently found these two genera confused in collections. Ulmer's (1907) monograph of the subfamily is still useful for some genera such as *Macronema* Pictet, but not for *Amphipsyche*; of the 22 species currently recognized only two were known to Ulmer. Kimmins (1962; 1963) described several African species, but new characters have been discovered in some of these.

The keys here provided to the Old World genera of Macronematini, and to the species of *Amphipsyche*, are based on external characters as far as possible, but several species are known only from males and critical examination of the genitalia is often necessary. Using a cladistic analysis of the species of *Amphipsyche* the genus is divided into three main species-groups. Some of the evolutionary and zoogeographical implications of this classification are discussed, and it is intended to apply this approach to other genera of the Macronematinae and ultimately to test the current generic and tribal groupings within the whole subfamily.

The methods of preparation and drawing of specimens are virtually the same as in the revision of the Polymorphanisini (Barnard, 1980). Temporary glycerine preparations of male and female genitalia were used for examination, and denuded wings were drawn from dry-mounted slide preparations wherever possible.

The scale lines on the figures represent the following lengths: wings 1·0 mm; maxillary palps 0·25 mm; legs 0·5 mm; genitalia 0·25 mm. All other features illustrated have their scale indicated on the figure. The arrows on some figures indicate features referred to in the keys or in the species descriptions.

The nomenclature of wing veins and genitalia components follows Schmid's (1980) broadly based study. This means that some of the names previously used in the Polymorphanisini revision are now changed. Thus the aedeagus is here termed the phallotheca, and the gonopods are now called the inferior appendages. The wing venation terminology is unchanged, except that the apical forks are labelled I to V. Thus fork R_2 is now fork I, fork R_4 is fork II, fork M_1 is fork III, fork M_3 is fork IV, and fork Cu_{1a} is fork V. These forks are the same in both the fore and hind wing (except that fork IV never occurs in the hind wing of Trichoptera).

No attempt has been made to homologize the endothecal spines of *Amphipsyche* males with those seen in some other genera. They are thus given the arbitrary names of dorsal, mid and ventral spines, according to their level of insertion on the apex of the phallotheca. The phallocrypt pocket may be homologous with the similar structure seen in some other families of Trichoptera (Nielsen, 1957), but its ontogeny is unknown.

Under the heading 'Material examined' for each species are listed only the total numbers of

each sex, the countries of collection and institutions holding the material. Full collection data are given only for type-specimens. Where there is further information on the distribution of a species which is not apparent from the list of material examined, this is noted in the corresponding 'Remarks' section.

Abbreviations of depositories

BMNH	British Museum (Natural History), London, U.K.
IP	Institut für Pflanzenschutzforschung, Eberswalde, D.D.R.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MCZ	Museum of Comparative Zoology, Harvard University, U.S.A.
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin, D.D.R.
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NAC	Nanjing Agricultural College, Nanjing, China
NM	Naturhistorisches Museum, Vienna, Austria
RNH	Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
RSM	Royal Scottish Museum, Edinburgh, U.K.
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.
ZI	Zoological Institute, Lund, Sweden
ZM	Zoologisches Museum, Hamburg, B.R.D.
ZSI	Zoological Survey of India, Calcutta, India

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Taxonomic method

Although the cladistic method of classification is often taken to be equivalent to Hennig's (1966) phylogenetic systematics, Platnick (1979) has pointed out that there is no necessary connection between cladistics and the process of evolution: a cladogram can be constructed simply by studying the pattern of the distribution of characters in a group of organisms. Although this 'transformed' cladistic approach has been criticized by several authors (e.g. Beatty, 1982) on the grounds that the claimed evolutionary neutrality is actually counter-productive, Platnick argued that cladistic methods are simply attempts to discover natural groups by analysing their characters, which is surely the aim of taxonomy in general.

One of the difficulties with Hennig's phylogenetic method is that the taxonomist has to make *a priori* decisions about the polarity of character states, and to sort them into apomorphies and plesiomorphies on the basis of outgroup comparisons. This is a crucial step in the construction of a phylogeny, because groups can be recognized only on the basis of synapomorphies. Inevitably, some of these decisions on the polarity of character states are very hard to make, because the taxonomist has to assume at least some of the evolutionary history of the group before he starts. There is thus an element of circularity in the process, because one cannot make such assumptions about characters used to produce a phylogeny, and then use that phylogeny to draw independent conclusions about the evolution of the group. Platnick (1979) argued that the 'plesiomorphic' state of a character is really the more general one, in that it is found in more

groups than the 'apomorphic', or less general, state. The group possessing the more specialized character state is therefore contained within the group showing the more general state, and this gives rise to the nested sets and subsets which form the hierarchical classification. This is an important concept, in that it avoids the idea that plesiomorphic and apomorphic states are alternatives: it also clearly shows why a group based on plesiomorphies alone cannot be a natural one because it would be recognized only by the absence of characters. Thus the production of a cladogram does not depend on the reconstruction of the evolutionary history of the group, but on the differentiation of more general characters from less general ones. The hierarchical structure of the cladogram is therefore a result of the inter-nested sets of unique characters, each delimiting a natural group.

The test of whether the taxonomist has correctly identified the level of generality of a character is whether or not it is congruent with other characters at higher and lower levels. Instead of making decisions about the polarity of character states, one has only to distinguish the presence of a character from its absence, the latter being hypothesized as the more general condition. This highlights the problem of using the loss of a character to delimit a group. Phylogeneticists would decide that a loss character may be apomorphic by *a priori* outgroup reasoning, whereas transformed cladists would discover the level of generality of the 'loss' by its congruence with all the other characters examined. In practice, however, it is preferable to use presence characters to recognize groups, because without ontogenetic data it is hard to distinguish the secondary loss of a character from its absence at a more general level, unless there is a high degree of congruence.

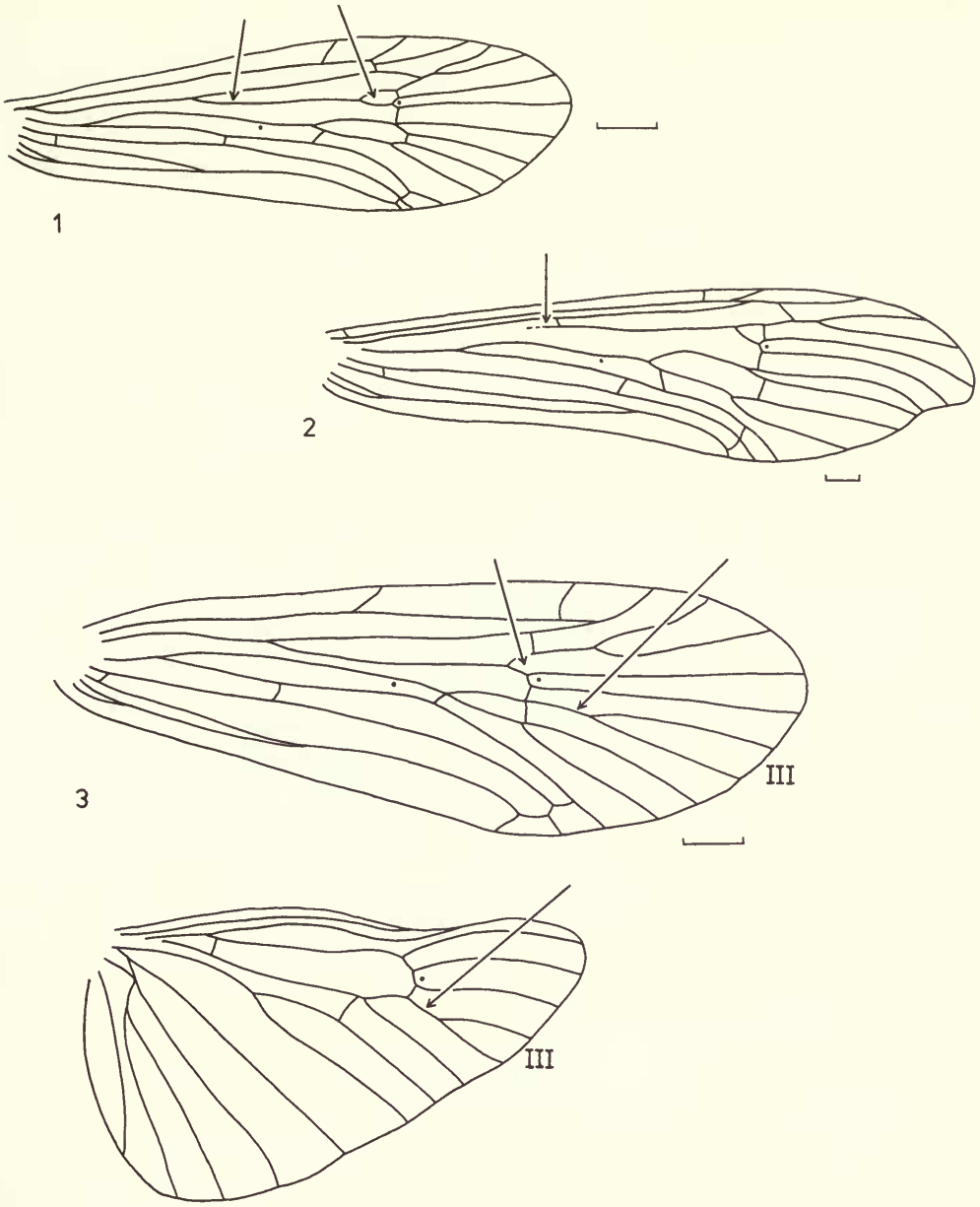
Having produced a cladistic classification without any assumptions of evolutionary history or speciation mechanisms, the taxonomist is then free to use the cladogram to infer something about the evolution of the group being studied, by hypothesizing a phylogenetic tree. Following the cladistic analysis of *Amphipsyche* I therefore discuss some of the phylogenetic and zoogeographic implications of the cladogram. The use of the transformed cladistic method and its application in biogeography are discussed in detail by Nelson & Platnick (1981).

Classification of the Macronematini

The current classification of the subfamily Macronematinae was discussed in a previous paper (Barnard, 1980). Of the two constituent tribes, the Polymorphanisini is almost certainly monophyletic, despite being delimited by loss characters. The adults are recognized by the loss of the mouthparts, and the larvae by the loss of the stridulatory organs on the head and fore legs (Scott, 1975). However, the tribe Macronematini lacks any diagnostic characters and is probably not monophyletic, although certain generic groups can be distinguished within it. For example, *Macrostemum* Kolenati, *Amphipsyche* and *Protomacronema* Ulmer can be grouped on both adult and larval characters (Scott, 1975), the most noticeable larval character being the raised carina on the head. The Neotropical genus *Blepharopus* Kolenati probably belongs here too (Flint & Wallace, 1980) although the carina is only poorly developed. On the other hand, the larvae of *Leptonema* Guérin-Méneville and *Macronema* s.str. (Flint & Bueno Soria, 1982) have no carina, but *Leptonema* and *Macrostemum* adults are often very similar superficially. More study is needed to clarify the validity of this tribe, but the group is retained here for convenience.

Key to Old World genera of Macronematini

1		Discoidal cell present in fore wing, but sometimes very small (Fig. 1)	2
–		Discoidal cell absent in fore wing (Fig. 3)	5
2	(1)	R_1 in hind wing ends on R_{2+3}, joined to *Sc* by short cross-vein (Fig. 9)	3
–		R_1 in hind wing fuses with *Sc* (Fig. 8)	4
3	(2)	In fore wing, base of *Rs* entire (Fig. 1)	***PSEUDOLEPTONEMA*** Mosely
–		In fore wing, base of *Rs* obsolete, joined to R_1 by cross-vein (Fig. 2)	***TRICHOMACRONEMA*** Schmid
4	(2)	Maxillary palp with second segment longer than third (Fig. 4)	***LEPTONEMA*** Guérin-Méneville

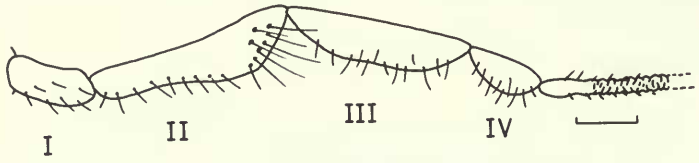


Figs 1–3 1, *Pseudoleptonema* sp. ♂, fore wing; 2, *Trichomacronema* sp. ♂, fore wing; 3, *Leptopsyche gracilis* McLachlan ♂, fore and hind wings.

– Maxillary palp with third segment longer than second (Fig. 5)..... ***MACROSTEMUM*** Kolenati
5 (1) Fork III in both wings with stalk (Fig. 3) ..... ***LEPTOPSYCHE*** McLachlan
– Fork III in both wings sessile (Figs 6, 7) 6
6 (5) ♂: anal area of fore wing strongly dilated (Fig. 12); ♀: *Sc* in hind wing ends on costal margin (Fig. 18) ..... ***AMPHIPSYCHE*** McLachlan
– ♂: anal area of fore wing not dilated (Fig. 6); ♀: *Sc* in hind wing fuses with R_1 to end on R_{2+3} (Fig. 7) ..... ***PROTOMACRONEMA*** Ulmer

AMPHIPSYCHE McLachlan

Amphipsyche McLachlan, 1872: 68. Type-species: *Amphipsyche proluta* McLachlan, by monotypy.
Phanostoma Brauer, 1875: 69. Type-species: *Phanostoma senegalense* Brauer, by monotypy. [Synonymized by Martynov, 1935: 201.]
Amphipsychella Martynov, 1935: 201. Type-species: *Amphipsychella extrema* Martynov, by original designation and monotypy. **Syn. n.**



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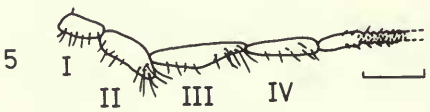
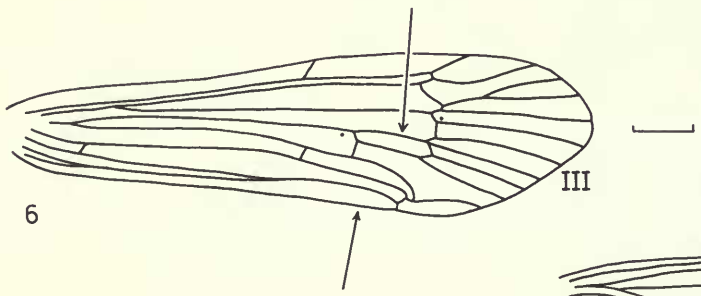
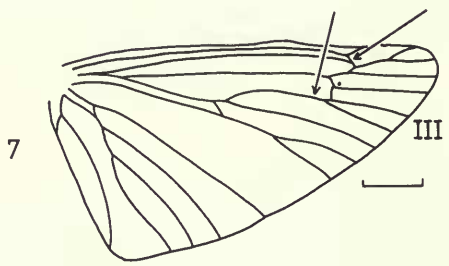
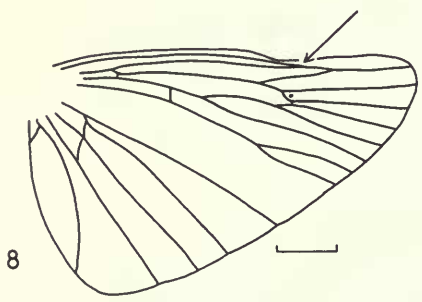
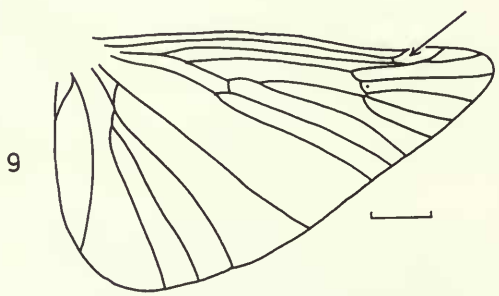










Figs 4–9 4, *Leptonema* sp., maxillary palp; 5, *Macrostemum* sp., maxillary palp; 6, *Protomacronema* sp. ♂, fore wing; 7, *Protomacronema* sp. ♀, hind wing; 8, *Macrostemum* sp. ♂, hind wing; 9, *Pseudoleptonema* sp. ♂, hind wing.

Small to medium sized species, wing length ♂ 8–20 mm, ♀ 6–15 mm, yellowish or brownish in colour, rarely with markings on head or thorax. Antenna up to three and a half times wing length in ♂, up to twice wing length in ♀; flagellar segments numerous (75–100 in ♂, 45–70 in ♀), always elongate. Head with two pairs of setigerous warts in ♂, hind pair indistinct, only one pair in ♀; genae in *apicalis*-group flat, with silverish pubescence. Maxillary palp with fifth segment usually very long and secondarily articulated, but sometimes reduced or even entirely fused with fourth segment. Spur formula basically 1.4.4, but often reduced to 0.4.4, 0.4.3, 0.4.2, 0.3.2 or 0.2.2. Tibia and tarsus of mid leg broad and flat in ♀. Wing-coupling mechanism consists of single row of curved macrotrichia on costal margin of hind wing, enaging on anal fold of fore wing (Fig. 10). Discoidal cell absent in fore and hind wings ('false' discoidal cell formed by secondary fusion of R_4 and R_5 in fore wing of *apicalis*); median cell present in fore wing, usually absent in hind wing (present in *magna*). In fore wing R_1 and *Rs* often sinuous near anastomosis; fork I always stalked, fork II usually sessile, but stalked in *apicalis*-group. *Sc* in hind wing ends on costal margin, joined to R_1 by cross-vein. ♂ fore wing with strong dilated anal area.

♂ genitalia with elongate two-segmented inferior appendages; phallocrypt pocket, associated with base of inferior appendages, and pre-anal appendages present in *proluta*-group only. Phallotheca usually with broad base, narrow stem and bulbous apex, with up to three pairs of endothecal spines. ♀ eighth sternite partially divided into two sclerites.

Remarks. Within the Macronematini, *Amphipsyche* seems most closely related to the African genus *Protomacronema*. Both genera have a very similar wing venation, although *Protomacronema* males do not have the dilated anal margin of the fore wing seen in *Amphipsyche*, and in the female hind wing *Sc* fuses with R_1 to end on R_{2+3}, instead of ending on the costal margin. The male genitalia are also superficially similar, *Protomacronema* having a pair of endothecal spines similar to those in the African species of *Amphipsyche*, but a detailed study of *Protomacronema* is needed in order to clarify the relationships of these two genera.

Amphipsyche and *Phanostoma* Brauer have always been considered as being closely related, and have usually been separated on the spur formula. Martynov (1935: 201) synonymized them on the grounds that the species within *Amphipsyche* showed such variation in the number of spurs that the two genera were essentially the same. This was not accepted by all later authors (e.g. Ulmer, 1951) but eventually Kimmins (1962) showed that the spur formula of *A. senegalensis* (the type-species of *Phanostoma*) had been wrongly described, and that the distinction between the genera could no longer be maintained. *Phanostoma* is available as a subgeneric name for the *meridiana*-group recognized in the current study, but such a formal subdivision of the genus does not seem necessary. Kimmins also suspected that *Amphipsychella* Martynov was a synonym of *Amphipsyche*, and although I have seen no specimens of *A. extrema*, I am confident that this synonymy is correct.

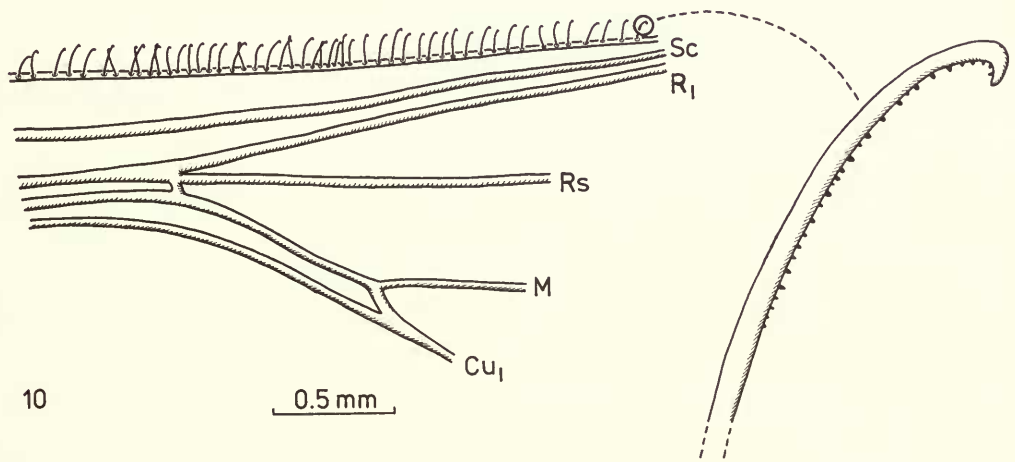


Fig. 10 *Amphipsyche berneri* ♂, wing coupling mechanism on costa of hind wing.

Geographical distribution

Most species of *Amphipsyche* are restricted to the Old World tropics. The *meridiana*-group has representatives throughout the Afrotropical region, Madagascar, India and Sri Lanka, and through mainland South East Asia to Java, Borneo and the Philippines. The *apicalis*-group is restricted to S. India, Burma, Thailand, Vietnam, West Malaysia, Sumatra and Borneo, and the *proluta*-group occurs only in India, China and the Amur region of the U.S.S.R. Some zoogeographical implications of these distributions are discussed below (p. 84).

A. senegalensis is the most widespread African species, being found throughout almost the whole of the Afrotropical region, whereas the other African species have very restricted distributions (Fig. 119). Similarly, *meridiana* is a very widespread species throughout India, Sri Lanka and South East Asia as far east as Java, although this distribution is apparently disjunct (Fig. 104). Most of the other species in the *meridiana*-group, and in the other groups, have more restricted distributions. The unique occurrence of *proluta* in central and northern China northwards to the Amur region of the U.S.S.R. shows an interesting parallel with *Aethaloptera evanescens* (McLachlan) in the Polymorphanisini (Barnard, 1980). There is a third species in the Macronematinae, *Macrostemum radiatum* (McLachlan), with a similar distribution, although this species extends into Siberia (like *A. evanescens*) and also occurs in Japan.

Biology

The first account of the immature stages of a species of *Amphipsyche* was by Hafiz (1937), who described the larva and pupa of *meridiana* (as *indica*) from material collected near Calcutta. Ulmer (1957) gave detailed descriptions of Javan and Sumatran larvae and pupae of *meridiana*, but these vary in some features from Hafiz' account. Hafiz described the larval head as being uniformly dark brown, whereas Ulmer described (and figured) a pair of yellow flecks extending from the eyes onto the frontoclypeus. I have examined larvae recently collected from Java and they match Ulmer's figures of the head markings, so this feature may represent a genuine difference between the populations in India and Indonesia. The two descriptions also vary in the gill formula (allowing for the fact that the two authors used slightly different terminology for some gills) but here the recently collected Javan material matched exactly Hafiz' description of Indian specimens. Further information is needed to determine whether this species is polymorphic or whether the two populations are perhaps subspecifically distinct.

The larva of *A. proluta* was described by Lepneva (1947: redescribed, 1970). Despite the two species being in different species-groups it is apparent that the larvae of *meridiana* and *proluta* resemble each other very closely, the main difference being that in *proluta* the yellow head markings fuse to form a continuous transverse band. The gill formula of *proluta* matches that of the recently collected specimens of *meridiana* from Java.

The larva of the African species *senegalensis* was first described from Ugandan material by Hickin (1955). Jacquemart (1957) gave a further detailed account of this species from Lake Edward (Zaire), but it should be noted that in his description the legends (and numbers) of the figures of the prothorax and mesothorax have been transposed, and the metathorax is figured upside-down. Ulmer (1963) described his Egyptian larval material as *curvinerve*, here considered a synonym of *senegalensis*. Ulmer's description seems to differ slightly from those of Hickin and Jacquemart, but he made no direct comparisons with these earlier accounts, and without seeing material from these different areas one cannot draw any conclusions. Ulmer gave the gill formula for his '*curvinerve*' specimens, which is quite different from those of *meridiana* and *proluta*, but as neither Hickin nor Jacquemart described the gills of *senegalensis*, further comparison is impossible. Moreover, Ulmer's specimens may have represented *ulmeri* Kimmins, and not '*curvinerve*'. The pupa of *senegalensis* was first figured and briefly described by Gibbs (1973), with a detailed description by Marlier (1978). Several aspects of the biology of *A. scottae* have been described in papers by Chutter and Scott (see below) and a full description of the larva appears in Scott (in press).

Although the larvae of only these few species have been described in any detail, there is sufficient in common between them to recognize some generic characters. This has been done by

Lepneva (1970), Gibbs (1973) and Scott (1975; in press), all of whom give characters sufficient to distinguish *Amphipsyche* larvae from those of other macronematine genera, especially *Macrostemum* (as *Macronema*), *Leptonema* and *Protomacronema*. Scott (1975) has demonstrated that the larvae of *Protomacronema* and *Amphipsyche* seem to show a close relationship between these two genera, thus confirming the evidence suggested by the adult characters (see 'Remarks' p. 77).

Ulmer (1957) separated the larvae of *Amphipsyche* and *Phanostoma* on the form of the hind tarsal claw. This was described as half the length of the tarsus and pointed in *Amphipsyche meridiana*, and only one-third the tarsal length and blunt in *Phanostoma*. This character was later figured in '*Phanostoma curvinerve*' (Ulmer, 1963). However, if Hickin's (1955) and Jacquemart's (1957) figures of *senegalensis* are accurate, the claw is also half the tarsal length and pointed in this species. It is possible that the short, blunt claw in Ulmer's specimens is due to excessive abrasion on a rocky substrate (which is known to affect both the anal and tarsal claws in other species of Trichoptera).

Habitats

Larvae of *Amphipsyche* are generally found in fast-flowing rivers on a stony substrate. Hickin (1955) also recorded *A. senegalensis* in Lake Victoria, but the larvae were near the outfall of the Nile and were therefore still in fast water. Scott (1970) found the same species in Lake Kariba, in a deep bay at the mouth of a stream, and Seshadri (1955) described the mass occurrence of *A. meridiana* in the very rapid water near the sluice gates of a reservoir.

Chutter (1963) described the ecological requirements of *A. scottae* in some detail. The species was found on the Vaal River in South Africa, immediately below the man-made Vaal Barrage. Here the larval population dropped in winter and built up again in September–November, presumably in direct response to the increase in zooplankton populations, although some larvae were present all the year round. Further down the same river Chutter (1968) found that most adults of this species were caught in January, when the larval populations were again low. The gut contents of some larvae showed that they are apparently omnivorous, feeding on algae as well as on insects such as *Simulium* larvae.

Boon (1979) discovered populations of *A. meridiana* below the artificial Lake Rawapening on the River Tuntang in central Java. Many organisms have difficulty in living in such a regulated river which is subject to sudden large changes in both water level and current speed. Parts of the substrate of this river are formed from vesicular volcanic lava, and large numbers of *meridiana* larvae live in the vesicles in the rock. Boon has suggested four advantages of this habitat: (1) the spacing of the vesicles enforces the spacing of the larvae, both within the same species and between the other two hydropsychid species in the same river, thus preventing overcrowding; (2) the fairly deep vesicles give protection against predation; (3) the larvae are protected from being dislodged during high water levels; (4) they are protected from desiccation during low water levels. Moreover, *meridiana* larvae also construct very tough feeding nets, which are more resistant to damage than those of most Hydropsychidae and also do not collapse in low current speeds or even when exposed at low water. Boon also showed that larvae apparently co-operate in building large communal nets, which is unusual in this family. It therefore seems that *meridiana* is a particularly adaptable species, and this may be linked to its widespread distribution through India, South East Asia and Indonesia. The fact that *senegalensis* has been found in both rivers and lakes (albeit always in fast water) suggests that it too may be an adaptable species, possibly accounting for its widespread Afrotropical distribution.

Corbet (1958*a*) studied the fauna of the Victoria Nile below the Owen Falls Dam, subsequent to the use of DDT to eliminate populations of the *Simulium damnosum* complex in an effort to control onchocerciasis. Trichoptera in general are very sensitive to DDT, and the previously large populations of *A. senegalensis* disappeared entirely from the treated stretch of river immediately after the addition of the insecticide. Over a year later the populations of *senegalensis* were still very small, despite the chance of recolonization from unaffected popula-

tions immediately upstream. Corbet showed that this kind of insecticidal treatment can have long-term effects on many such macroinvertebrates as well as on the fish which rely on them for food.

'Pest' species

Where *Amphipsyche* larvae have colonized the fast, zooplankton-rich water immediately below man-made reservoirs and impoundments, either the larvae or the adults have sometimes reached 'pest' proportions. Seshadri (1955) gave an account of *meridiana* larvae occurring below the sluice gates of a reservoir in India. Here the adults were the problem, flying in enormous numbers every night between September and November, swarming around the street-lights and causing a great nuisance to people living nearby. Seshadri vividly describes how 'By about 8 P.M. it was a remarkable sight to see these insects in their millions dashing against lamps, and dropping to the ground so as to cause considerable annoyance to passers-by and vehicles. This went on throughout the night and every morning, to the Town Sanitary Staff fell the task of cleaning up the streets and removing basket loads of dead insects, especially from under the fluorescent lamps, where they formed shallow heaps several inches thick and many square feet in extent.' The larval nets were found encrusting the rocks for a few hundred yards downstream of the sluice gates and at times of low water the decaying stranded larvae were 'emanating a foul stench all over the entire locality'. Hickin (1955) described the 'peculiar sickly odour' of the dead bodies of vast numbers of adults of *senegalensis* which, together with a species of *Cheumatopsyche* Wallengren, had been swarming around a light at the Ripon Falls, Lake Victoria. Adults of *senegalensis*, together with a mayfly, were the main insect nuisance at the lights of the Owen Falls Dam (Uganda) according to Corbet (1958*a*), and he also (1958*b*) reported that larvae of *senegalensis* and two *Cheumatopsyche* species occasionally occurred in such numbers as to obstruct filters in the same dam.

Flight activity

The flight period of *Amphipsyche* species, like that of most Trichoptera, is virtually continuous in the tropics, but more noticeably seasonal in the more temperate regions. For example, *A. meridiana* adults are found in virtually every month of the year, whereas *scottae* adults, in South Africa, have been captured mainly from December to March.

Corbet & Tjønneland (1955) studied the flight activity of different species of Trichoptera throughout the night. The general pattern was of two peaks, one at dusk and one at dawn, although not every species exhibited both peaks of activity. *A. senegalensis* was exceptional in flying throughout the night, with no recognizable peaks; this species also flies in daylight. Only females of *senegalensis* were caught, which led Corbet (1966) to postulate that this species may be parthenogenetic. However, light-trap catches often show abnormal sex ratios because of differential attraction to light, and the material examined in the present study contains appreciable numbers of males of this species, many caught at light. Corbet's claim therefore seems unjustified, although facultative parthenogenesis cannot be ruled out.

Cladistic analysis

The list of characters used in the analysis is given below, grouped under broad morphological divisions. They are all 'presence' characters (see p. 74) and the state of the absence of the character is given in parentheses after each one. In the data matrix (Table 1) their presence is indicated by a plus sign and their absence by a dash, and the order of characters is re-arranged to show how the groupings were constructed to produce the cladogram (Fig. 11). Two apomorphic loss characters could have been used in this analysis, but are unnecessary. The *meridiana*-group can be recognized by the loss of the fore tibial spurs and by the hind spurs being reduced to two or three. The spur formula of 1.4.4 in the *proluta*- and *apicalis*-groups is demonstrably plesiomorphic for the genus (by outgroup comparison with the other genera in the tribe) but the presence of character 21 is sufficient to distinguish the *meridiana*-group, making such phylogenetic reasoning unnecessary. The list of characters used is as follows.

Head

1 Vertex with dark brown markings (no markings)
2 Genae flat with silverish pubescence (rounded with no pubescence)
3 Fifth segment of maxillary palp simple (annulated)
4 Fourth and fifth segments of maxillary palp fused (separate)

Thorax

5 Mesoscutellum with pair of dark markings (no markings)

Fore wing

6 Anal margin dilated in male (margin straight)
7 Fork II stalked (sessile)
8 'False' discoidal cell present (absent)
9 Fork I with dark marking (no marking)
10 Series of dark spots at wing apex (no spots at apex)
11 Sc–R_1 cross-vein with dark marking (no marking)
12 Diagonal marking proximal to anastomosis (no marking)

Hind wing

13 M_{3+4}–Cu_{1a} cross-vein present (absent)

Male genitalia

14 Ninth segment with lateral row of setae (only dorsal row present)
15 Phallocrypt pocket present (absent)
16 Basal segment of inferior appendage broad distally (narrow distally)
17 Basal segment of inferior appendage entirely broad (entirely narrow)
18 Inferior appendage with median setigerous projection on inner side (no setigerous projection)
19 Ventral apex of phallotheca produced (apex rounded)
20 Ventral apex of phallotheca pointed (apex rounded)
21 Phallotheca with ventral median groove meeting gonopore (no groove)
22 Eversible endotheca present (no endotheca)
23 Base of phallotheca flattened dorso-ventrally (base rounded)
24 Base of phallotheca extended into two pointed lobes (base rounded)
25 Base of phallotheca broadly triangular (base rounded)
26 Stem of phallotheca thickened in lateral view (stem narrow)
27 Ventral endothecal spines present (absent)
28 Mid endothecal spines present (absent)
29 Dorsal endothecal spines present (absent)
30 Dorsal leaf-like lobes on phallotheca (lobes absent)
31 Mid endothecal spines blunt, rod-like (spines pointed)
32 Mid endothecal spines very long and thickened (spines short and narrow)
33 Mid endothecal spines fused (spines paired)
34 Mid endothecal spines sharply up-turned (spines straight or only slightly curved)

Three species were not included in the cladistic analysis. *A. bengalensis* and *extrema* were omitted because I was unable to examine material, and *delicata* because males of this species are unknown (male genitalic characters constitute over half the characters used in the analysis). *A. bengalensis* and *extrema* belong to the *meridiana*-group on the basis of their spur formulae (that of *bengalensis* probably being wrongly quoted – see p. 112). The male genitalia of *bengalensis*, which seem to have only the mid endothecal spines present, modified into blunt rods, also place the species in this group, presumably near to *sinhala*. Little can be surmised about *extrema* as it is known only from Martynov's figures of the female, but the highly reduced spur formula and shortened maxillary palps would suggest that it may also be closely related to *sinhala*. Although specimens of *delicata* have been examined, the affinities of the species are doubtful as it possesses none of the non-genitalic characters used in the analysis; it also has the intermediate spur formula of 0.4.4. I suspect that it belongs in the *proluta*-group; it cannot belong in the *apicalis*-group because it lacks characters 2, 7 and 9, and its Chinese distribution makes its inclusion in the *meridiana*-group unlikely, though not impossible.

Table 1 Data matrix used in the construction of the cladogram (Fig. 11).

Species	Character																														
	25	12	4	34	20	11	33	26	32	24	3	31	19	5	23	29	30	27	28	21	8	22	10	18	2	7	9	1	17	13	15	16	14	6
berneri	+	−	+	−	−	+	−	+	+	−	+	-	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
corbeti	+	−	+	−	−	+	−	+	+	−	+	−	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
fuscata	−	+	+	−	−	+	−	+	+	−	+	−	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
scottae	−	−	−	−	+	+	−	+	+	−	+	−	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
ulmeri	−	−	−	+	+	+	−	+	+	−	−	−	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
instabilis	−	−	+	−	−	−	+	+	+	−	+	−	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	+	−	−	−	+
pellucida	−	−	−	−	−	−	−	−	−	+	+	−	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	+	+
sinhala	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
meridiana	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
parva	−	−	?	−	−	−	−	−	−	−	?	−	−	−	+	+	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
magna	−	−	−	−	−	−	−	−	−	−	+	−	−	+	+	+	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
senegalensis	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−		−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
exsiliens	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	+	+	−	−	−	−	−	+	+
apicalis	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+	+	−	−	+	+	+	−	−	−	−	−	+	+
gratiosa	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	+	+	+	+	−	−	−	−	−	−	+
petiolata	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	−	−	−	−	−	+	+
distincta	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	+	+	−	+
bifasciata	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	+	+	+	+
proluta	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+

Incongruencies in the cladogram

Although the cladogram shown is the most parsimonious one that can be constructed from the available data, there are a number of apparent incongruencies in the data matrix (Table 1) to which attention is drawn. Character 11 delimits a distinct group of African species (Fig. 11) but this wing-marking also occurs in *senegalensis* and *exsiliens*. However, its appearance in *senegalensis* is not consistent, and in *exsiliens* it is part of the broader stripe across the anastomosis. Character 19, the produced ventral apex of the phallotheca, delimits a large section of the *meridiana*-group, and also occurs in *apicalis*, but the phallotheca of this species is different in all other respects. Character 30, the presence of leaf-like lobes on the phallotheca, occurs in both *meridiana* and *gratiosa*, but each lobe in *gratiosa* is distinctive in bearing a spine at its tip. Thus each of these apparent incongruencies probably arises from the non-homology of the character, and no real doubt is cast on the validity of the groups suggested by the cladogram.

Character 13, the M_{3+4}–Cu_{1a} cross-vein in the hind wing, occurs independently in *instabilis* and *proluta*, and can thus be considered convergent for these two species.

The remaining three incongruencies are of more interest in that they may highlight some real difficulties. Character 14, the presence of a row of lateral setae on the ninth abdominal segment of the male, is used to combine the *proluta*- and *apicalis*-groups. However, the character is absent in *gratiosa* and *distincta*, yet it occurs independently in *pellucida* of the *meridiana*-group. Only the discovery of further characters at the same level of generality can test the validity of this

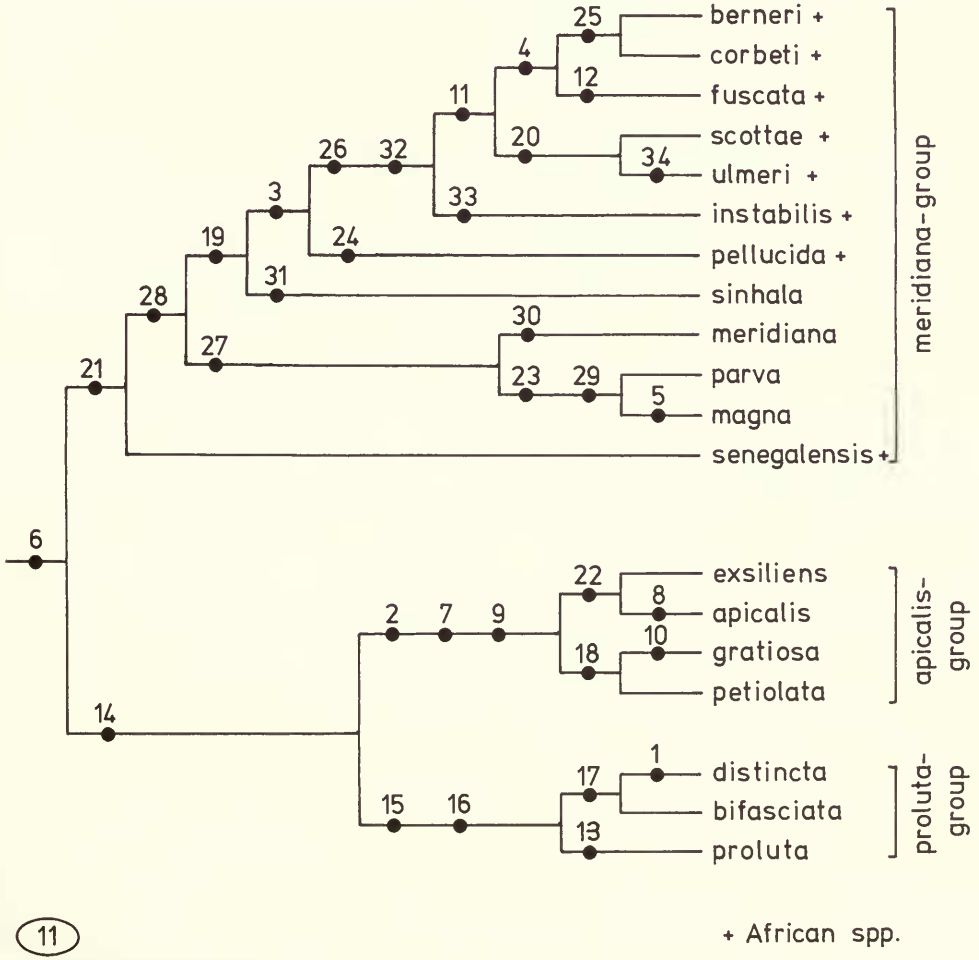


Fig. 11 Cladogram of *Amphipsyche* species.

group. Character 4, the fusion of the 4th and 5th segments of the maxillary palp, delimits the *berneri–corbeti–fuscata* subgroup, yet this character is also seen in *instabilis*. Similarly, character 3, the lack of secondary articulation on the 5th segment of the maxillary palp, appears to delimit the 'African' subgroup of the *meridiana*-group (excluding *senegalensis*); however, this character does not occur in *ulmeri* but is seen in *magna*. Again, these incongruencies may indicate incorrect groupings in the cladogram, or else possible homoplasy; it seems reasonable to suggest that character 4 in *instabilis* and character 3 in *magna* have each arisen independently, as this tendency for simplification and reduction of the maxillary palps is well known in other genera of the Macronematinae.

Thus there is still scope for further testing of the groups hypothesized in the cladogram, and the discovery of more characters, perhaps in the larvae, is needed to confirm or modify these groupings. Such extra data will show whether the incongruencies arise from non-homology of a character, from the usage of the character at the wrong level of generality, or whether homoplasy can be demonstrated in this genus.

It will be noted that several of the individual species do not have autapomorphies indicated on the cladogram. All of these species are easily recognized, as is demonstrated in the key to species, but they do not have easily described unique features which will differentiate them from all other species in the genus rather than merely from their nearest neighbour. Thus *berneri* and *corbeti* can be distinguished from each other by the lobes of the male tenth segment, which are broad and divergent in *berneri* but narrow and sub-parallel in *corbeti*. Neither of these character states would distinguish one or other species from all others in the genus, and their use would generate confusion and repetition in the cladogram.

Evolutionary and zoogeographical considerations

The geographical distributions of the main species-groups and some of their components have been outlined earlier (p. 78). In brief, the three species-groups have noticeably different distributions, although all three overlap to some degree. It is interesting to try and deduce something of the evolutionary history of the genus from these data, coupled with the information from the cladogram (Fig. 11). For these purposes the cladogram can be considered as a phylogram, showing degrees of common ancestry (Nelson & Platnick, 1981: 171), although branching points do not denote actual speciation events or real ancestors.

The current distribution of the genus in Africa, Madagascar, India and South East Asia suggests that it arose when the African, Malagasy and Indian land-masses were still closely associated, namely before the end of the Cretaceous (Smith, Hurley & Briden, 1981). Each of these three components carried its own fragmented group of species, and the further dispersal and evolution of the genus would have occurred when India became linked with South East Asia (Late Eocene/Oligocene).

This kind of model seems more useful than postulating the origin of the genus in one of the three main areas of its distribution (Africa, India, South East Asia) with subsequent long-range dispersal to the other two. Several other macronematine genera have similar widespread distributions, such as *Polymorphanisus* Walker, *Aethaloptera* and *Macrostemum* (the latter also occurring in the New World), and their long-range dispersal seems similarly unlikely in view of their relatively limited powers of flight and their restriction to certain freshwater habitats. Some other genera of the subfamily are restricted to one continent; *Protomacronema*, which may be the sister-group of *Amphipsyche* is found only in Africa, and future studies on these genera should indicate whether or not this model is satisfactory.

The *meridiana*-group of *Amphipsyche* has representatives in Africa, Madagascar, India and South East Asia, but it is important to note that not all the African species form a monophyletic group. *A. senegalensis* was apparently an early coloniser of Africa, where it is now the most widespread species (Fig. 119), but all the other African species (including *pellucida* from Madagascar) form a monophyletic group with allopatric distributions. Each member of this sub-group is individually sympatric with *senegalensis*, which tends to confirm their more distant relationship with that species (Nelson & Platnick, 1981: 384). The *apicalis*- and *proluta*-groups

have no African representatives but both occur in India and South East Asia. It thus seems likely that both arose from a common Indian ancestral species, and that each group later dispersed and speciated throughout South East Asia, along with some members of the *meridiana*-group.

Check-list of *Amphipsyche* species

Although most of the species in this list are arranged according to the relationships suggested by the cladistic analysis (Fig. 11), they are not phyletically sequenced (Wiley, 1981: 211). This is partly because three species, *bengalensis, delicata* and *extrema*, were omitted from the cladogram owing to lack of suitable material; these species would be *sedis mutabilis* sensu Wiley. Moreover, the cladogram is not of the simple asymmetrical 'pectinate' type which lends itself to this sequencing convention without the proliferation of formal subgroup names.

AMPHIPSYCHE McLachlan
- *Phanostoma* Brauer
- *Amphipsychella* Martynov **syn. n.**

***proluta*-group**
- ***proluta*** McLachlan
  - *paraproluta* Hwang **syn. n.**
- ***bifasciata*** Navás
- ***distincta*** Martynov
- ***delicata*** Banks

***apicalis*-group**
- ***apicalis*** Banks
- ***exsiliens* sp. n.**
- ***gratiosa*** Navás
- ***petiolata*** Ulmer
  - *minima* Banks **syn. n.**
  - *pubescens* Kimmins **syn. n.**

***meridiana*-group**
- ***senegalensis*** (Brauer)
  - *curvinerve* (Navás) **syn. n.**
- ***magna*** Banks
- ***parva*** Banks
- ***meridiana*** Ulmer
  - *nirvana* Banks **syn. n.**
  - *vedana* Banks **syn. n.**
  - *propinqua* Ulmer **syn. n.**
  - *indica* Martynov **syn. n.**
  - *tricalcarata* Martynov
  - *sigmosa* Navás **syn. n.**
- ***sinhala* sp. n.**
- ***bengalensis*** Martynov
- ***extrema*** (Martynov) **comb. n.**
- ***pellucida*** (Navás) **comb. n.**
- ***instabilis*** Kimmins
  - *plicata* (Jacquemart) **syn. n.**
- ***ulmeri*** Kimmins
- ***scottae*** Kimmins
- ***fuscata*** Kimmins
- ***corbeti*** Kimmins
- ***berneri*** Kimmins

Key to species of *Amphipsyche*

Of necessity this key is based largely on features of the male genitalia, which are often the only reliable way of distinguishing species in this genus; moreover, the females of nine of the species are unknown. However, geographical distribution and external characters such as wing venation and spur formulae are used where feasible, so that isolated female specimens can be identified as far as possible.

1		Spur on fore tibia absent	2
–		Spur on fore tibia present	16
2	(1)	Four spurs on hind tibia; ♀; R_1 in fore wing ends on *Sc* (Fig. 39) (♂ unknown) ***delicata*** (p. 93)	
–		Two or three spurs on hind tibia; R_1 in fore wing ends on wing margin	3
3	(2)	♂: phallotheca with three pairs of endothecal spines (Fig. 82)	4
–		♂: phallotheca with only two pairs of endothecal spines or less	5
4	(3)	Very large species, fore wing 15–20 mm; pair of round markings on mesoscutellum (Fig. 87) (Philippines) ***magna*** (p. 102)	
–		Small species, fore wing 8 mm; no markings on mesoscutellum (♀ unknown) (Borneo) ***parva*** (p. 105)	
5	(3)	Indian or Sri Lankan species	6
–		African or Malagasy species	9
6	(5)	♀: maxillary palps very short (Fig. 116); only one or two spurs on mid tibia (♂ unknown) ***extrema*** (p. 112)	
–		Maxillary palps unmodified; four spurs on mid tibia	7
7	(6)	Spurs 0.4.2	8
–		Spurs 0.4.3 or 0.4.4 ***meridiana*** (p. 106)	

8	(7)	♂: endothecal spines rod-like, longer than breadth of phallotheca stem (Fig. 117) (♀ unknown) (India) ..... ***bengalensis*** (p. 111)
–		♂: endothecal spines much shorter than breadth of phallotheca stem (Fig. 98) (Sri Lanka) ..... ***sinhala*** (p. 105)
9	(5)	Hind tibia with three spurs; ♂: base of phallotheca extended into two pointed lobes (Fig. 134) (Malagasy species) ..... ***pellucida*** (p. 115)
–		Hind tibia with two spurs; ♂: phallotheca of other shape (Afrotropical species) 10
10	(9)	♂: endothecal spines absent (Fig. 124) ..... ***senegalensis*** (p. 112)
–		♂: at least one endothecal spine present 11
11	(10)	Cross-vein present between M_{3+4} and Cu_{1a} in hind wing (Figs 140, 147); ♂: mid endothecal spines fused into single structure (Fig. 145) ..... ***instabilis*** (p. 117)
–		No such cross-vein in hind wing; ♂: mid endothecal spines paired 12
12	(11)	♂: fifth segment of maxillary palp fused with fourth (line of fusion visible in *fuscata*, Fig. 167); apex of phallotheca rounded (Fig. 175) 13
–		♂: fifth segment of maxillary palp distinct (sometimes reduced in length); apex of phallotheca pointed (Fig. 159) 15
13	(12)	♂: diagonal fuscous marking on fore wing (Fig. 165); base of phallotheca narrow (Fig. 169) (♀ unknown) ..... ***fuscata*** (p. 123)
–		♂: no diagonal wing marking; base of phallotheca broadly triangular (Fig. 175) 14
14	(13)	♂: lobes of tenth segment broad and divergent in dorso-ventral view (Fig. 180) (♀ unknown) (Ghana) ..... ***berneri*** (p. 127)
–		♂: lobes of tenth segment narrow, subparallel in dorso-ventral view (Fig. 176) (♀ unknown) (Uganda) ..... ***corbeti*** (p. 125)
15	(12)	♂: mid endothecal spines gently curved dorsally (Fig. 159) (South Africa) .. ***scottae*** (p. 121)
–		♂: mid endothecal spines turned abruptly dorsally (Fig. 154) (♀ unknown) (Sudan) ..... ***ulmeri*** (p. 120)
16	(1)	Genae flat with silverish pubescence; fork II stalked in fore wing (Fig. 54) 17
–		Genae rounded with no pubescence; fork II sessile in fore wing (Fig. 12) 20
17	(16)	'False' discoidal cell in fore wing (enclosing corneous spot) (Fig. 43) (India) ... ***apicalis*** (p. 94)
–		No 'false' discoidal cell 18
18	(17)	♂: phallotheca with eversible endotheca (Figs 59, 60) (♀ unknown) (Burma) ***exsiliens*** (p. 96)
–		♂: phallotheca without eversible endotheca 19
19	(18)	Fore wing with striking pattern of five dark brown spots with other paler brown markings (Fig. 61); ♂: phallotheca with large dorsal leaf-like lobes (Fig. 65) (♀ unknown) ..... ***gratiosa*** (p. 98)
–		Fore wing with only one dark brown spot in fork I (Fig. 68); ♂: phallotheca with no dorsal lobes (Fig. 72) ..... ***petiolata*** (p. 99)
20	(16)	Cross-vein present between M_{3+4} and Cu_{1a} in hind wing (Fig. 12) ..... ***proluta*** (p. 86)
–		No such cross-vein in hind wing 21
21	(20)	Vertex of head, antennal scape and pedicel with dark brown markings (Fig. 30) ***distincta*** (p. 89)
–		No markings on head (♀ unknown) ..... ***bifasciata*** (p. 89)

The *proluta*-group

Genae rounded, with no pubescence. Fork II sessile in fore wing. Spurs usually 1.4.4 but subject to reduction. Fifth segment of maxillary palp long and secondarily annulated. ♂ interior appendages with basal segment broad, at least distally; phallocrypt pocket present; pre-anal appendages present though small (absent in *distincta*). Phallotheca lacking endothecal spines. Ninth segment with two rows of setae (dorsal and lateral) in lateral view.

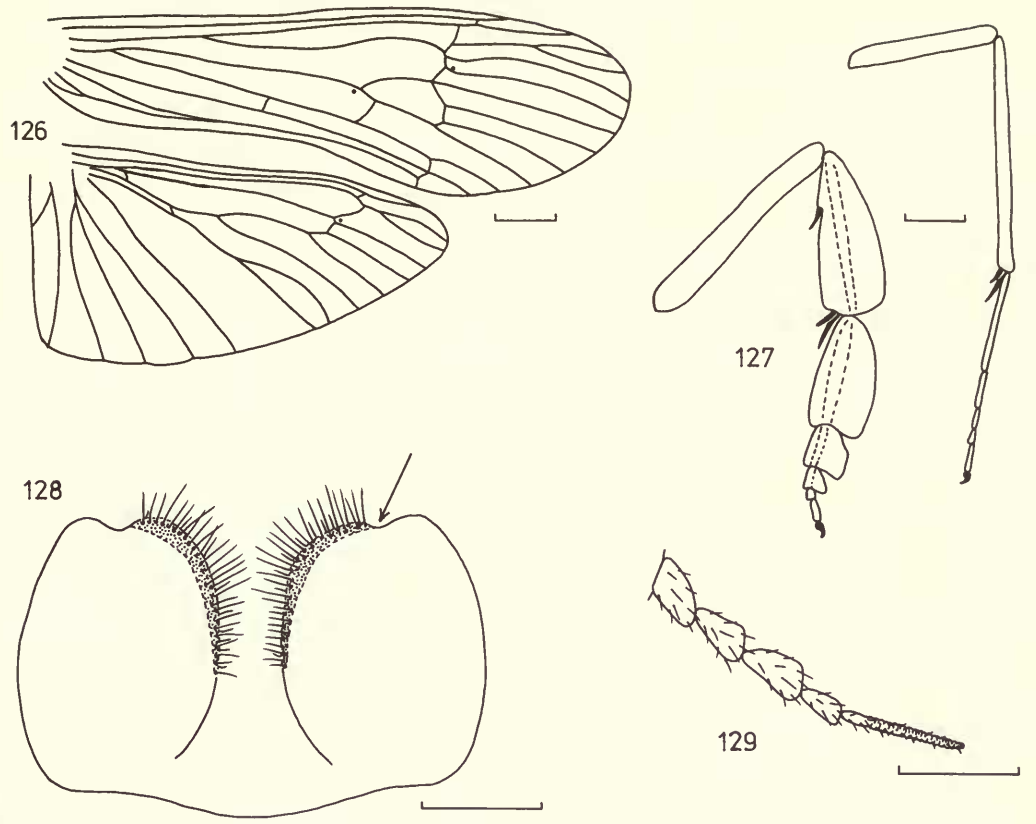
India, China and U.S.S.R. (Amur region).

Amphipsyche proluta McLachlan

(Figs 12–21)

Amphipsyche proluta McLachlan, 1872: 70. Lectotype ♂, U.S.S.R. (BMNH), designated by Kimmins, 1957*b*: 105 [examined].

Amphipsyche paraproluta Hwang, 1957: 387. Holotype ♂, China: Jiangsu Prov., Nanjing, 15.viii.1956 (*Hwang*) (NAC) [not examined]. **Syn. n.**



Figs 126–129 *Amphipsyche senegalensis* ♀. 126, wing venation; 127, mid and hind legs; 128, eighth sternites; 129, maxillary palp.

and Ulmer (1963) (as *curvinerve*); the pupa was described by Gibbs (1973) and Marlier (1978).

In addition to the distribution records below, Navás (1923) also recorded this species from Madagascar, but this is unconfirmed.

MATERIAL EXAMINED

Lectotype ♂ of *senegalensis*, **Senegal**: 1869 (*Steindachner*) (NM). Lectotype ♀ of *curvinerve*, **Egypt**: Cairo, 20.vii.1916 (*Alfieri*) (USNM).

79 ♂, 194 ♀, 3 larvae, 3 pupae, **Chad, Sudan, Ethiopia, Ghana, Nigeria, Cameroun, Zaire, Uganda, Tanzania, Zambia, Malawi, Zimbabwe, South Africa** (Transvaal) (BMNH, IRSNB, MRAC, RSM, USNM, ZI).

Amphipsyche pellucida (Navás) comb. n.

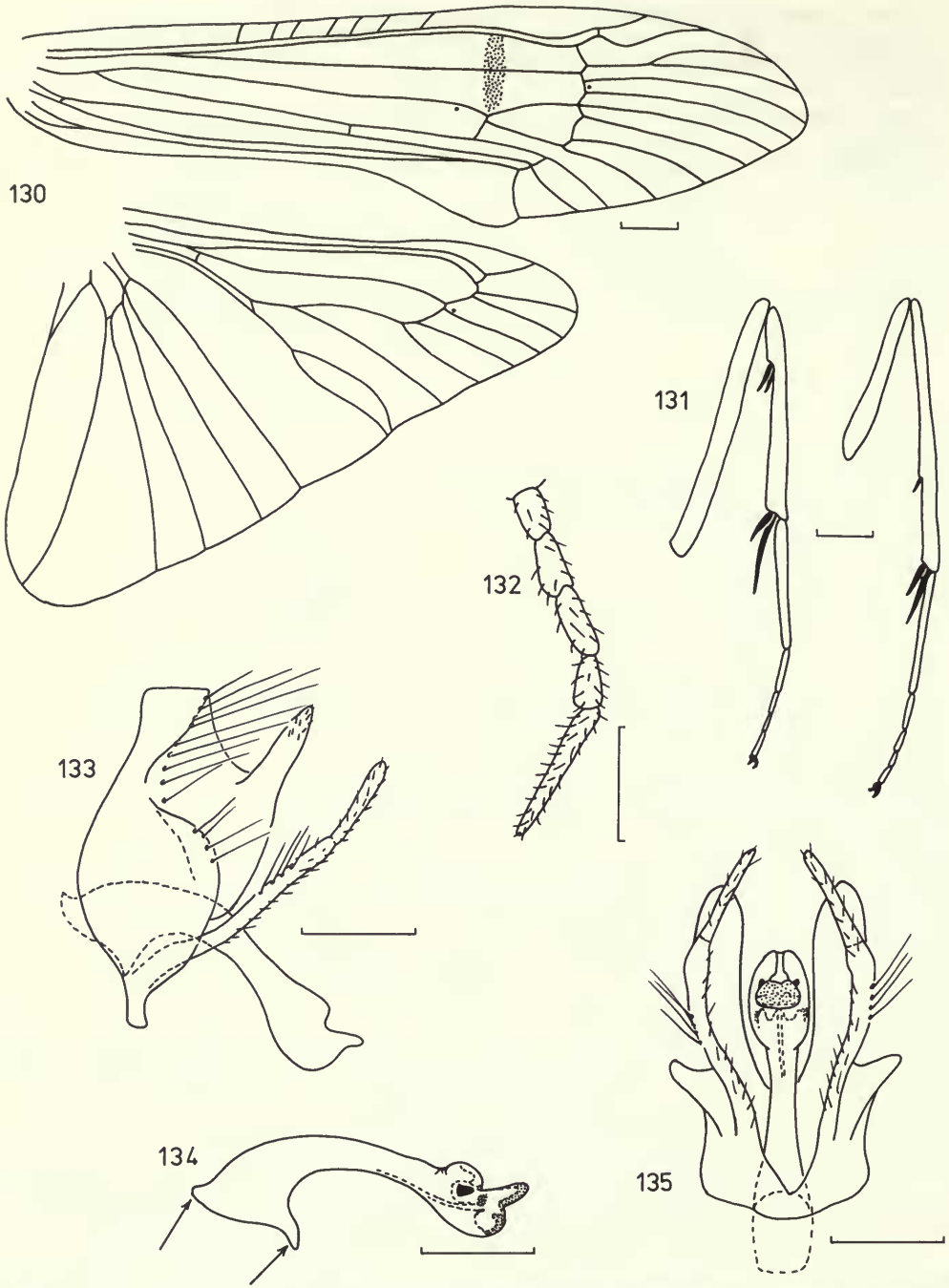
(Figs 130–139; distribution, Fig. 119)

Protomacronema pellucidum Navás, 1923: 26. Holotype ♀, MADAGASCAR (MNHN) [examined].

♂. Antenna 45 mm, with *c.* 80 segments. Fore wing 15–16 mm. Body yellowish brown; basal antennal segments annulated with dark brown, apical segments fuscous. Fore wing very pale yellow, with faint darker stripe from R_1 to M in line with M–Cu_1 cross-vein. Venation as in Fig. 130. Spurs 0.4.3 (Fig. 131). Maxillary palp 5-segmented, 5th segment not secondarily annulated, shorter than segments 1–3 combined (Fig. 132).

♀. Antenna 15 mm, with *c.* 60 segments. Fore wing 11–13 mm. Coloration as in ♂. Fore wing with no markings, venation as in Fig. 136. Spurs 0.4.3 (Fig. 137). Maxillary palp similar to that of ♂ (Fig. 139).

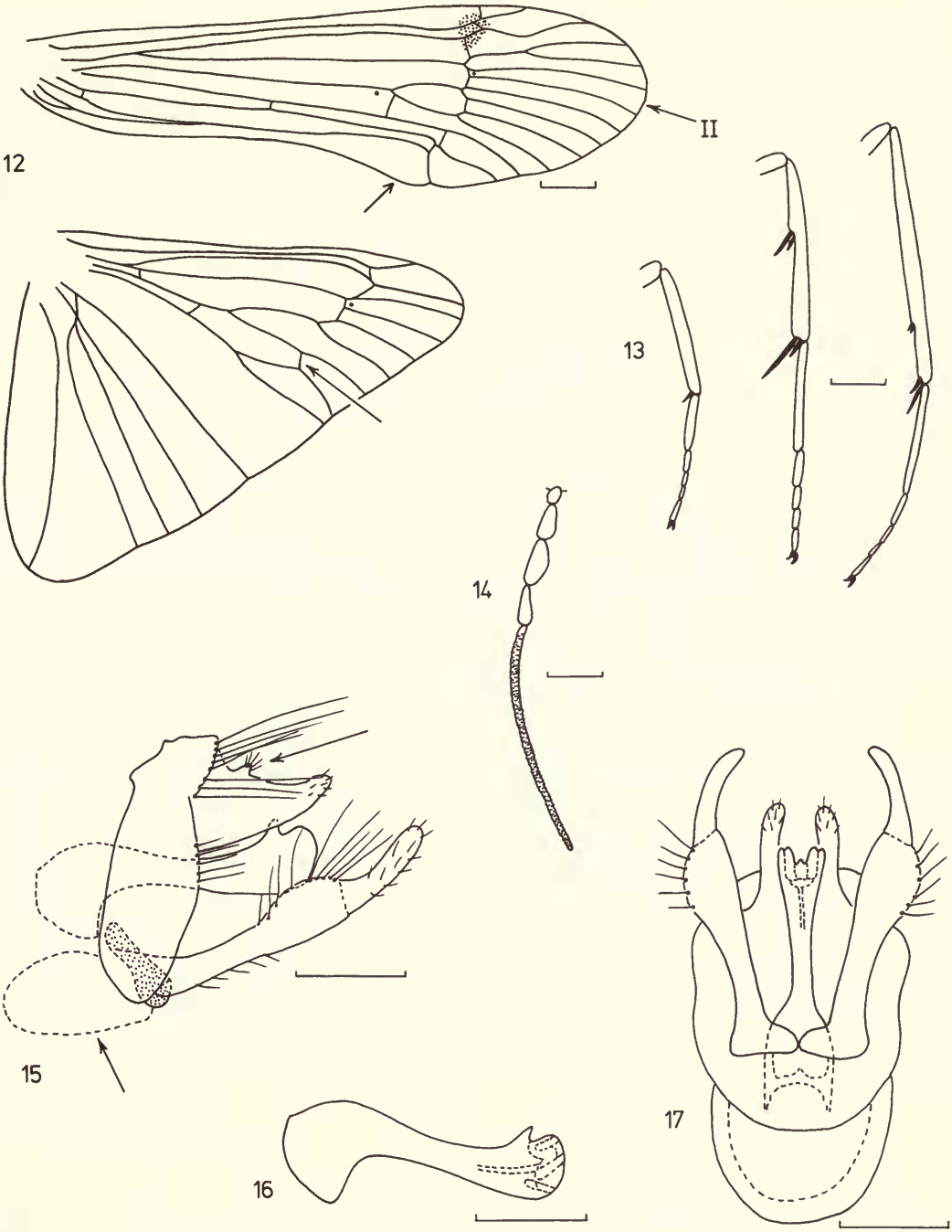
GENITALIA ♂ (Figs 133–135). Ninth segment broadly rounded laterally. Base of phallotheca narrow, with



Figs 130–135 *Amphipsyche pellucida* ♂. 130, wing venation; 131, mid and hind legs; 132, maxillary palp; 133, genitalia, lateral view; 134, phallotheca, lateral view; 135, genitalia, ventral view.

basal corners produced into pointed lobes. Stem of phallotheca narrow, apex produced into an elongate lobe. Only mid endothecal spines present, very short and blunt. Inferior appendage slender and sinuous, terminal segment clearly differentiated.

GENITALIA ♀ (Fig. 138). Eighth sternites oval, each sclerite almost symmetrical, with all corners rounded.



Figs 12–17 *Amphipsyche proluta* ♂. 12, wing venation; 13, legs; 14, maxillary palp; 15, genitalia, lateral view; 16, phallotheca, lateral view; 17, genitalia, ventral view.

♂. Antenna *c.* 30 mm, with *c.* 80 segments. Fore wing 11–14 mm. Body pale yellowish brown, antenna pale yellow, narrowly annulated with brown, becoming more fuscous towards antennal apex. Fore wing very pale yellow, with slightly darker marking around Sc–R_1 cross-vein, sometimes extending further onto anastomosis. Venation as in Fig. 12; cross-vein present between M_{3+4} and Cu_{1a} in hind wing. Spurs 1.4.4;

pre-apical spurs on hind tibia very short (Fig. 13). Maxillary palp 5-segmented, 5th segment secondarily annulated, over 1·5 times length of segments 1–4 combined (Fig. 14).

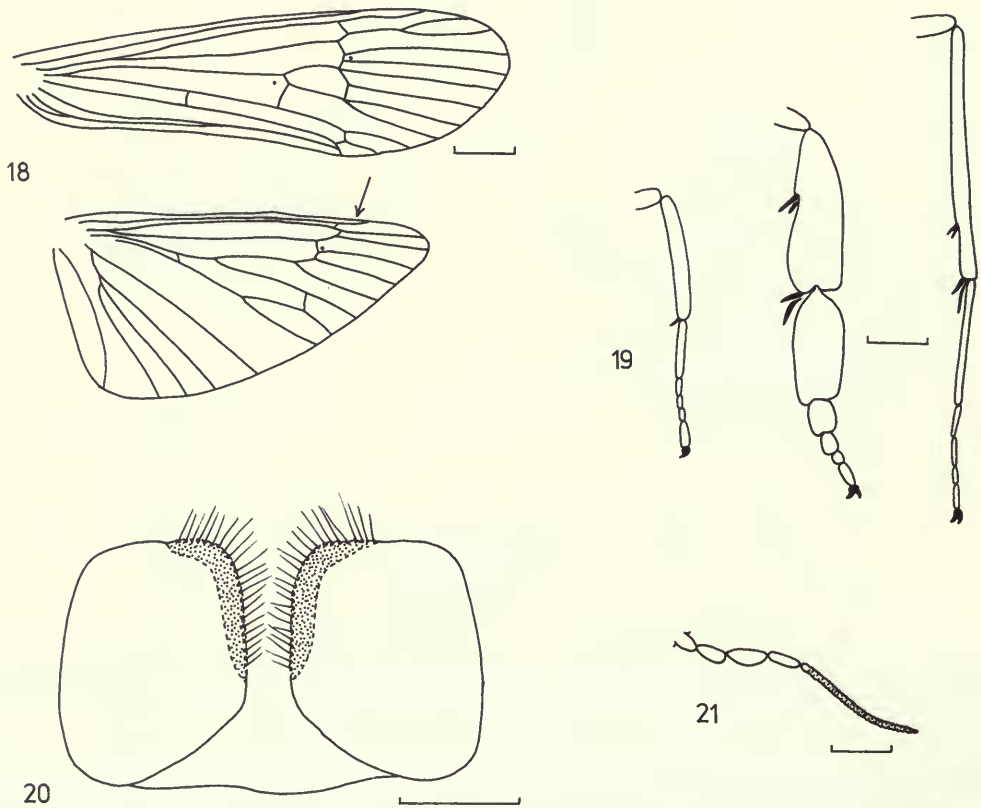
♀. Antenna *c.* 12 mm, with *c.* 50 segments. Fore wing 8–10 mm. General coloration as in ♂, fore wing with no dark markings. Venation as in Fig. 18; M_{3+4}–Cu_{1a} cross-vein in hind wing, as in ♂. Spurs 1.4.4 (Fig. 19). Maxillary palp similar to that of ♂, but 5th segment approximately same length as segments 1–4 combined (Fig. 21).

GENITALIA ♂ (Figs 15–17). Ninth segment narrow laterally, pre-anal appendages present as small setigerous projections on tenth segment (Fig. 15). Phallocrypt pocket relatively broad and rounded(Fig. 15). Basal segment of inferior appendage broad apically only, terminal segment partly differentiated. Phallotheca slender with narrow base; apex truncate, with slightly pointed lobe dorsally.

GENITALIA ♀ (Fig. 20). Eighth sternites broad, squarish; thickened inner margins wide, extending far down inner edges.

REMARKS. Although easily identified by the male genitalia, both sexes of this species can be distinguished from the rest of the *proluta*-group by the M_{3+4}–Cu_{1a} cross-vein in the hind wing. The only other species to show this character is *instabilis,* in the *meridiana*-group.

Hwang (1957) described *paraproluta* as differing from *proluta* in the male genitalia. However, it seems that he had only McLachlan's original description on which to base his comparison, and both McLachlan's description and figure of *proluta* are very poor. McLachlan saw only dried material, and the pointed valves, which he thought were the intermediate appendages, are apparently the tenth segment. McLachlan's (1878: 352) redescription of the species was rather better, with a clearer figure; here he noted the setigerous pre-anal appendage as 'a distinct tooth'. McLachlan's type-series of three males and two females is extant in the BMNH, although Kimmins (1957*b*) did not mention this in his lectotype designation.



Figs 18–21 *Amphipsyche proluta* ♀. 18, wing venation; 19, legs; 20, eighth sternites; 21, maxillary palp.

Although Hwang's (1957) description was apparently based on one male holotype, I was lent a male specimen from NAC labelled as paratype, which had identical data to the type. Whether or not this specimen has any type-status, it is an important 'topotypic' specimen, and examination of it confirmed the synonymy of *paraproluta* with *proluta*.

Three specimens examined (MNHN, MCZ) are labelled 'Hanlséon', apparently from China, according to Navás (1914). However, this is an impossible combination of letters for a Chinese place-name, and the label data must have been mis-copied from another, presumably hand-written, source. I tentatively suggest that the 'ls' is a misreading of the single (handwritten) letter 'k', and the final 'n' a misreading of 'u'. This would give the more plausible transliteration of 'Hankéou', the French spelling of Han-kow, for material collected by the Frenchman, de Guerne.

The larva of *proluta* was described by Lepneva (1947; 1970).

MATERIAL EXAMINED

Lectotype ♂ of *proluta*, **U.S.S.R.**: 'Amur Land' (*Maack*) (BMNH).

19 ♂, 8 ♀, **U.S.S.R.**: Amurskaya (2 ♂, 2 ♀ paralectotypes of *proluta*), **China** (1 ♂ 'paratype' of *paraproluta*) (BMNH, MCZ, MNHN, NAC).

Amphipsyche bifasciata Navás

(Figs 22–27)

Amphipsyche bifasciata Navás, 1931*a*: 7. Holotype ♂, CHINA: 'méridionale' (*Bris*) (lost).
[*Amphipsyche proluta* McLachlan; Banks, 1940: 207; Mosely, 1942: 361. Misidentifications.]

♂. Antennal length unknown (both specimens damaged). Fore wing 10–15 mm. Antennal segments pale yellow, with golden brown annulations. Head, thorax and abdomen yellowish brown. Fore wing pale yellow, shaded pale brown at apex and with darker brown stripe across anastomosis. Venation as in Fig. 22; fork I in fore wing approximately equal in length to its stalk. Spurs 1.4.4 (Fig. 24). Maxillary palp 5-segmented, 5th segment secondarily annulated, longer than segments 1–4 combined (Fig. 23).

♀. Unknown.

GENITALIA ♂ (Figs 25–27). Ninth segment relatively narrow laterally; pre-anal appendages present as small setigerous projections on tenth segment. Phallocrypt pocket elongate and sac-like in lateral view, shield-shaped in ventral view (Fig. 27). Basal segment of inferior appendage very broad, viewed laterally and ventrally; terminal segment clearly differentiated. Phallotheca slender, apex truncate, with pair of pointed unsclerotized lobes (superficially resembling endothecal spines); dorsally a single pointed lobe.

REMARKS. Well-marked examples of this species are easily recognized by the wing markings, but the single male examined from Szechwan has lost virtually all these markings, and is easily confused with *proluta*, hence Banks's (1940) misidentification.

According to the original description the holotype of *bifasciata* should be in Navás's collection, now in Barcelona, but when this was examined in 1979 the type was apparently missing (T. R. New, pers. comm.). However, Navás's illustration of the wing is sufficient to identify the species; it is obvious from his figure that the type is a male, although Navás does not mention this.

MATERIAL EXAMINED

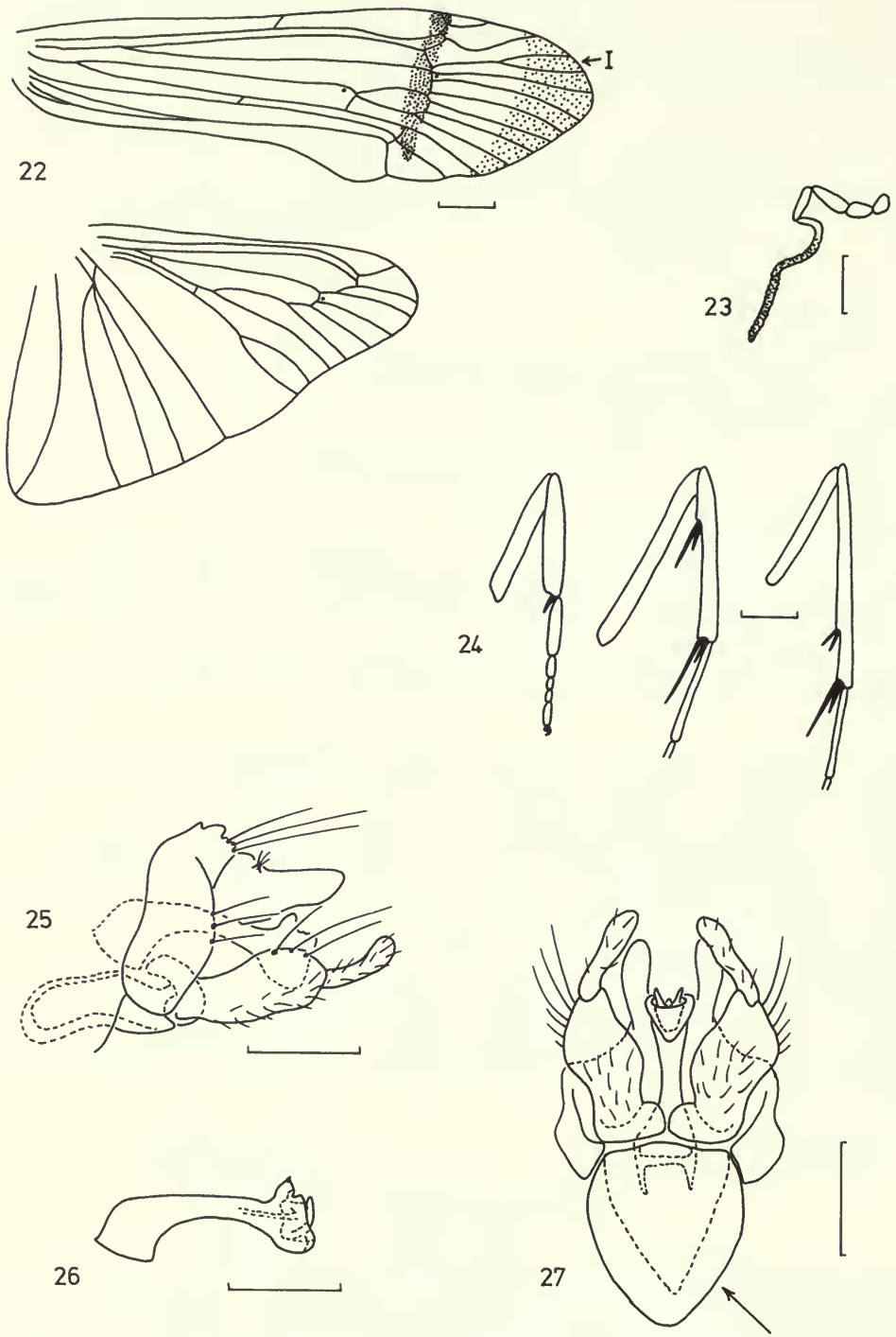
2 ♂, **China** (BMNH, USNM).

Amphipsyche distincta Martynov

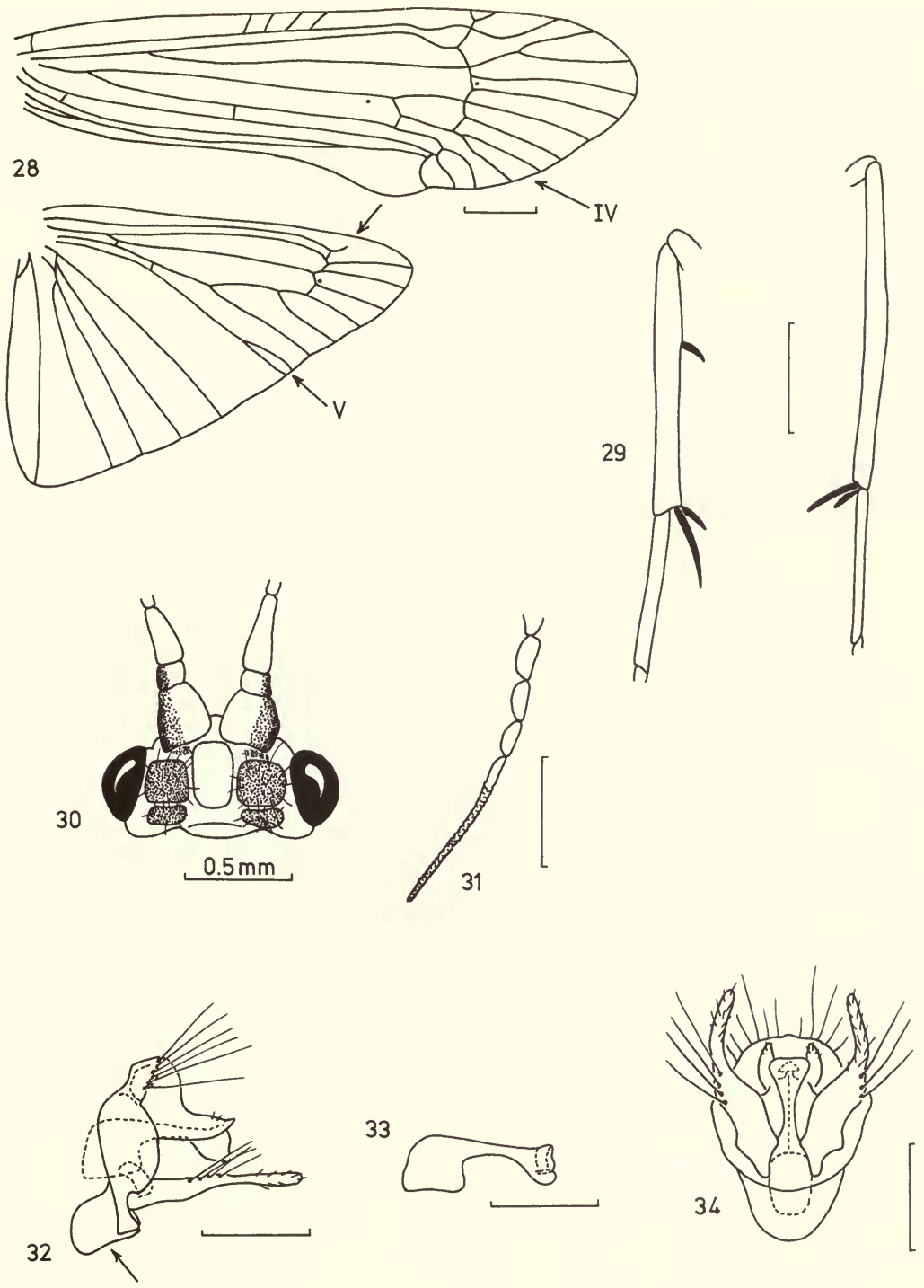
(Figs 28–38)

Amphipsyche distincta Martynov, 1935: 196. 6 ♂ syntypes, INDIA: Madhya Pradesh, river at Mandla, Nerbudda Survey (*Pruthi*) (lost from ZSI).

♂. Antenna up to 25mm, with *c.* 80 segments. Fore wing 8–10 mm. Body pale yellowish brown; setigerous warts on vertex of head dark greyish brown; antennal scape and pedicel with dark brown longitudinal stripe on dorsal surface (Fig. 30); front femur dark brown. Fore wing pale yellow, no dark markings. Venation as in Fig. 28; in fore wing fork IV with short stalk; in hind wing *Sc* not reaching wing



Figs 22–27 *Amphipsyche bifasciata* ♂. 22, wing venation; 23, maxillary palp; 24, legs; 25, genitalia, lateral view; 26, phallotheca, lateral view; 27, genitalia, ventral view.



Figs 28–34 *Amphipsyche distincta* ♂. 28, wing venation; 29, mid and hind tibiae; 30, head, dorsal view; 31, maxillary palp; 32, genitalia, lateral view; 33, phallotheca, lateral view; 34, genitalia, ventral view.

margin, fork V very narrow. Spurs 0.3.2 (Fig. 29). Maxillary palp 5-segmented, 5th segment secondarily annulated, longer than segments 1–4 combined (Fig. 31).

♀. Antenna up to 10 mm, with *c.* 50 segments. Fore wing 6–8 mm. Coloration as in ♂. Venation as in Fig. 35; in fore wing R_1 ends on *Sc*, fork IV sessile. In hind wing Cu_1 not forked, 2A absent. Spurs (Fig. 36) and maxillary palp (Fig. 37) as in ♂.

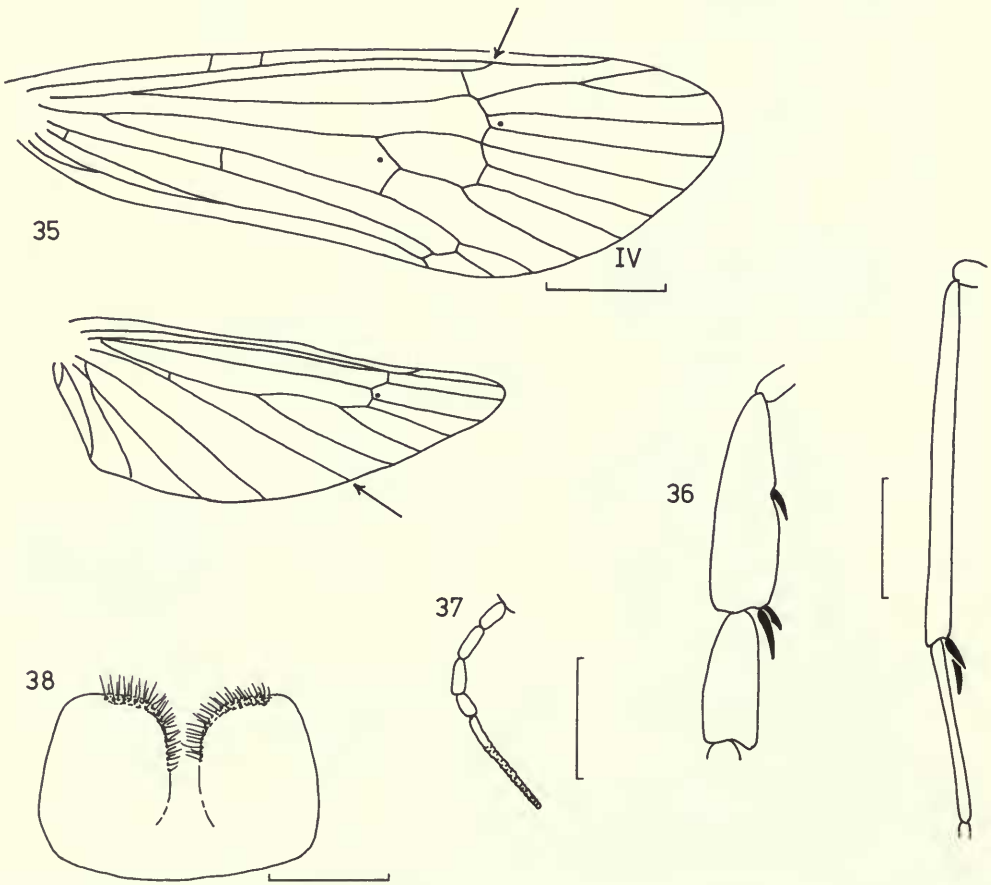
GENITALIA ♂ (Figs 32–34). Ninth segment broad laterally, pre-anal appendages absent. Phallocrypt pocket rounded in lateral view (Fig. 32), broadly triangular in ventral view. Inferior appendage broad and sinuous in ventral view, terminal segment not differentiated. Phallotheca broad basally, with narrow stem; apex triangular with no obvious appendages or lobes.

GENITALIA ♀ (Fig. 38). Eighth sternites broad, with squarish corners; thickened inner margins extending barely half length of sclerites.

REMARKS. This aptly named species is so distinctive that it is easily recognized; no other species has markings on the head and antennae (the only other species with any body markings is *magna*, with a pair of spots on the mesoscutellum).

Banks (1939) redescribed *distincta*, drawing attention to the dark front femur in both sexes. Martynov had described all the legs as being pale, but since all six syntypes are apparently lost (Ghosh, *in litt.*) this character cannot be checked on Martynov's material. Banks also stated that fresh specimens were 'plainly greenish'.

Martynov listed as the syntypes '4 ♂' followed by '2 ♂' with identical data; one of these may



Figs 35–38 *Amphipsyche distincta* ♀. 35, wing venation; 36, mid and hind tibiae; 37, maxillary palp; 38, eighth sternites.

be an error for '♀'. No descriptions of the female are given in his text, but this is also true of his description of *indica* (= *meridiana*), where both males and females make up the type-series.

A neotype designation does not seem necessary for such an easily recognizable species.

MATERIAL EXAMINED

19 ♂, 28 ♀, **India** (MCZ, USNM).

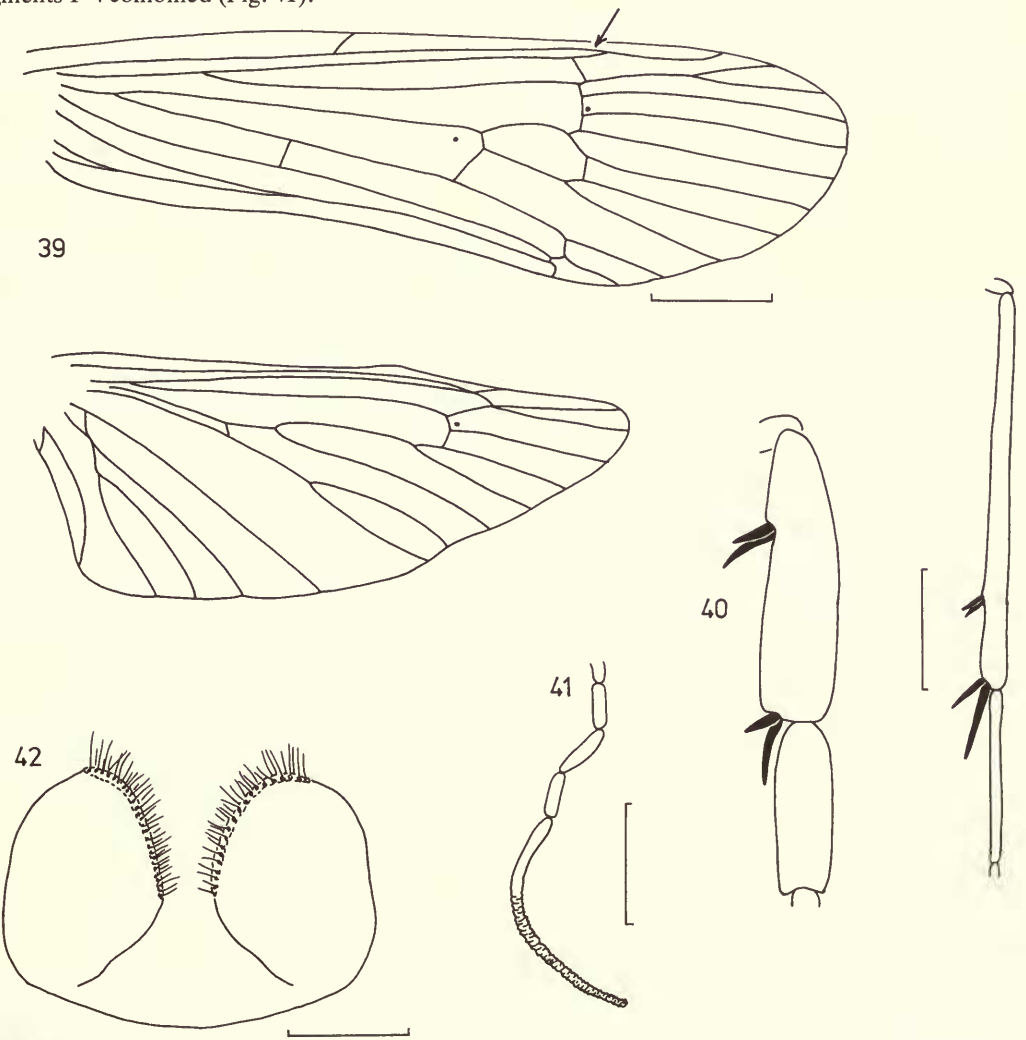
Amphipsyche delicata Banks

(Figs 39–42)

Amphipsyche delicata Banks, 1939: 58. LECTOTYPE ♀, CHINA (MCZ), here designated [examined].

♂. Unknown.

♀. Antenna over 12 mm, with more than 50 segments (all specimens damaged). Fore wing 6–8 mm. Antennal segments pale yellow, slightly annulated with brown. Head, thorax and abdomen yellowish brown. Fore wing very pale yellow with no markings, venation as in Fig. 39. R_1 in fore wing ends on *Sc*. Spurs 0.4.4 (Fig. 40). Maxillary palp 5-segmented, 5th segment secondarily annulated, longer than segments 1–4 combined (Fig. 41).



Figs 39–42 *Amphipsyche delicata* ♀. 39, wing venation; 40, mid and hind tibiae; 41, maxillary palp; 42, eighth sternites.

GENITALIA ♀ (Fig. 42). Eighth sternites rounded, bluntly pointed posteriorly; thickened inner edge relatively narrow.

REMARKS. The relationships of this species are in some doubt, mainly because no males have yet been discovered. Banks (1939) compared it with *minima* (= *petiolata*), from which it differs in venation, and with *distincta*, which he distinguished by the dark fore femora. It seems to be most closely related to *distincta*, with which it shares the venational feature of R_1 ending on *Sc* in the fore wing; this may be a synapomorphy for this pair of species. However, the placing of this species in the *proluta*-group is complicated by its unique spur formula of 0.4.4. It cannot belong in the *apicalis*-group because of the sessile fork II in the fore wing, and its Chinese distribution and unmodified maxillary palps make its inclusion in the *meridiana*-group unlikely.

The specimen here designated as lectotype was labelled 'type' by Banks, but not so published.

MATERIAL EXAMINED

Lectotype ♀, **China**: Hainan Tao I., Chung Kon, 18.vii.1935 (*Gressitt*) (type no. 23470, MCZ).
6 ♀ (paralectotypes), **China** (MCZ).

The *apicalis*-group

Genae flat, with silverish pubescence. Fore wing with fork II stalked, dark marking in fork I. Spurs always 1.4.4. Fifth segment of maxillary palp long and secondarily annulated (except ♀ *apicalis*). ♂ inferior appendages slender; phallocrypt pocket and pre-anal appendages absent. Phallotheca lacking endothecal spines. Ninth segment with two rows of setae as in *proluta*-group.

India, Burma, Thailand, Vietnam, West Malaysia, Sumatra and Borneo (Sarawak).

Amphipsyche apicalis Banks

(Figs 43–53)

Amphipsyche apicalis Banks, 1939: 56. LECTOTYPE ♂, INDIA (MCZ), here designated [examined].

♂. Antenna over 20 mm, with more than 50 segments (broken in both specimens examined). Fore wing 12–13 mm. Antennal segments pale golden brown, becoming more fuscous towards apex, slightly annulated with brown. Head, thorax and abdomen yellowish brown. Fore wing golden yellow, with dark brown spot in fork I, glabrous brown streaks at wing apex proximal to dark spot and across anastomosis (Fig. 43). In fore wing 'false' discoidal cell enclosing corneous spot at base of R_{4+5}, fork I with short stalk. R_{2+3} fused in hind wing. Spurs 1.4.4, pre-apical spurs on hind tibia short (Fig. 44). Maxillary palp 5-segmented, 5th segment secondarily annulated, longer than segments 1–4 combined (Fig. 45).

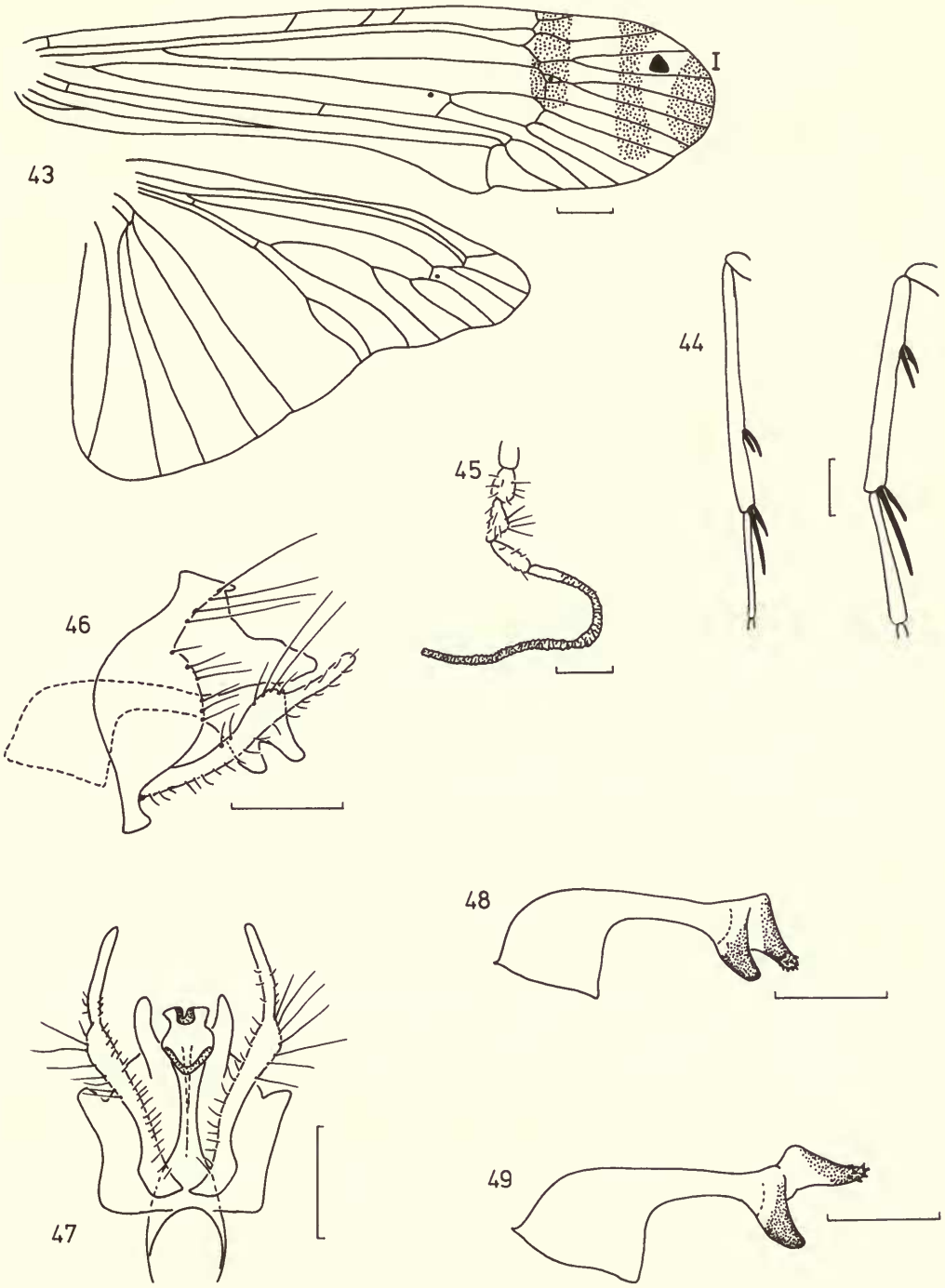
♀. Antenna over 12 mm, with more than 50 segments (broken in both specimens examined). Fore wing 9–10 mm. Body coloration as in ♂. Fore wing yellowish brown with pale brown spot on wing margin in fork I and another at anterior end of anastomosis (Fig. 50). Fore wing with 'false' discoidal cell as in ♂, but not so clearly defined. Spurs 1.4.4, one pre-apical spur on hind tibia very small (Fig. 51). Maxillary palp 5-segmented, 5th segment not annulated, approximately equal in length to segments 1 and 2 combined (Fig. 52).

GENITALIA ♂ (Figs. 46–49). Ninth segment with enlarged rounded side-pieces. Phallotheca with slender stem, enlarged apically to form two ventrally directed subtriangular processes; apical process with fine teeth at ventral apex, and hingeing dorsally to form a simple eversible endotheca (Figs 48, 49). Inferior appendage with pronounced setigerous projection mid-dorsally; terminal segment not clearly differentiated.

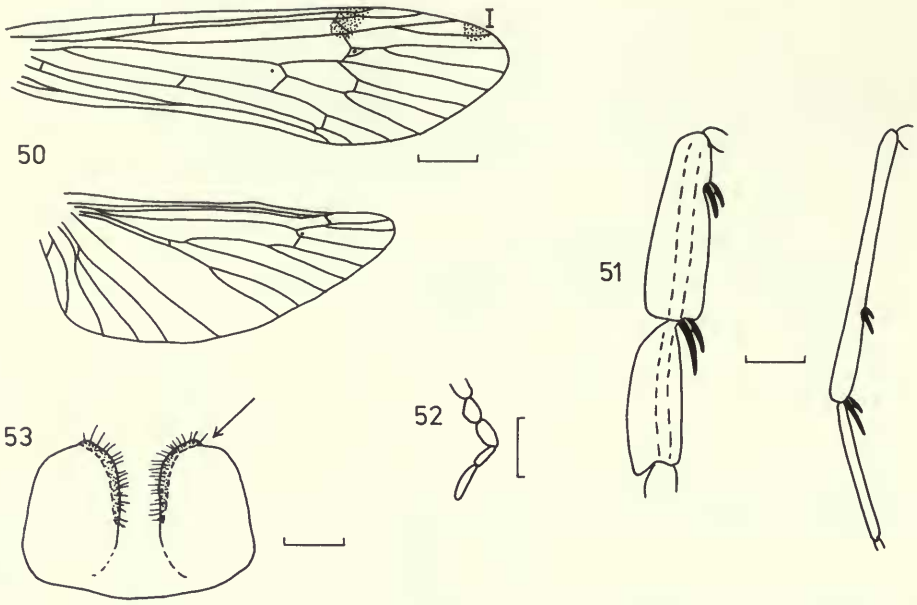
GENITALIA ♀ (Fig. 53). Eighth sternites with sharp indentation in posterior edge.

REMARKS. Superficially this species is very similar to *exsiliens* and *petiolata*, but is easily distinguished by the characteristic shape of the male phallotheca (Fig. 48).

Banks (1939) was unsure whether the two females from Coimbatore belonged to this species, but after examination of his material there seems little doubt that they are correctly placed here. Banks apparently overlooked the 'false' discoidal cell in the females (which is admittedly less obvious than in the males), and he also did not notice the very small pre-apical spur on the hind tibia. The faint wing markings in the female are a reduced form of the pronounced male pattern;



Figs 43–49 *Amphipsyche apicalis* ♂. 43, wing venation; 44, mid and hind tibiae; 45, maxillary palp; 46, genitalia, lateral view; 47, genitalia, ventral view; 48, phallotheca, lateral view; 49, phallotheca with endotheca everted.



Figs 50–53 *Amphipsyche apicalis* ♀. 50, wing venation; 51, mid and hind tibiae; 52, maxillary palp; 53, eighth sternites.

this is also seen in *petiolata*, and probably also in the closely related *gratiosa* and *exsiliens*, but the females of the last two species have yet to be discovered.

The specimen designated as lectotype was labelled 'type' by Banks, but not so published.

MATERIAL EXAMINED

Lectotype ♂, **India**: Mysore, Shimoga, R. Tunga, 1865′ [560 m], at light, 10.vi. [not iv as stated by Banks] [year unknown] (*Nathan*) (type no. 22677, MCZ).

1 ♂ (paralectotype), 2 ♀, **India** (MCZ).

Amphipsyche exsiliens sp. n.

(Figs 54–60)

♂. Antennal length unknown (broken in all specimens). Fore wing 12–14 mm. Body yellowish brown, back of head and dorsal surface of thorax brown; antennal segments pale yellow, narrowly annulated with brown. Fore wing pale yellow with brown spot in fork I and another centred on Sc–R_1 cross-vein; pale brown stripe across anastomosis and very pale shading at wing apex. Venation as in Fig. 54. Spurs 1.4.4 (Fig. 55). Maxillary palp 5-segmented, 5th segment secondarily annulated, longer than segments 1–4 combined (Fig. 56).

♀. Unknown.

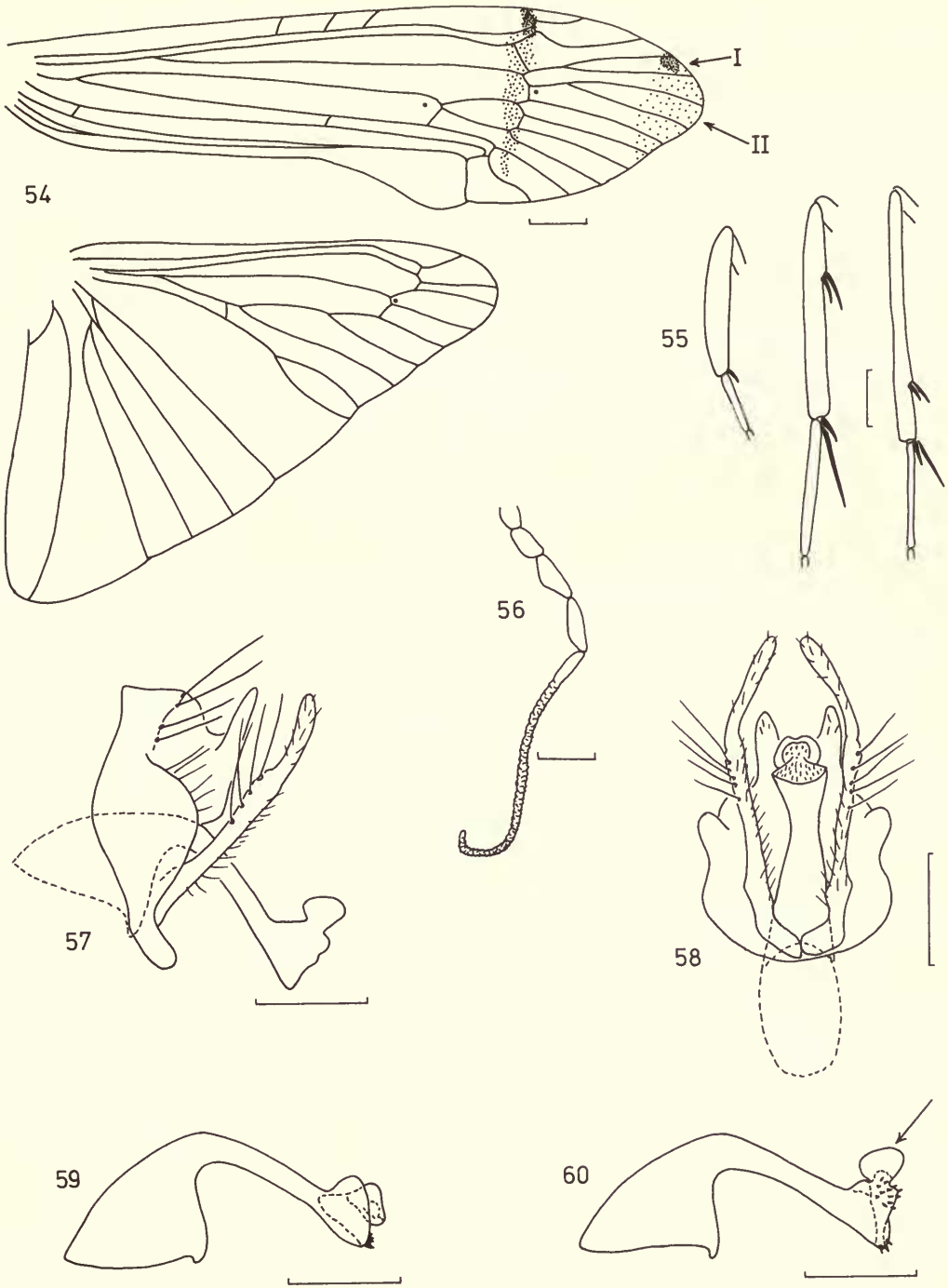
GENITALIA ♂ (Figs 57–60). Ninth segment broad laterally. Base of phallotheca broadly triangular, stem slender with triangular apex. Eversible sac-like endotheca present, connective membrane bearing many small spines (Fig. 60). Inferior appendage slender, terminal segment scarcely differentiated.

REMARKS. This species is easily distinguished from the other members of the *apicalis*-group by the rounded sac-like endotheca, which is more mobile than that of *apicalis*. In the latter species it hinges through only a few degrees, but in *exsiliens* it can be invaginated almost entirely inside the phallotheca apex, or hinged through almost 180° to lie dorsal to the apex (Figs 59, 60).

MATERIAL EXAMINED

Holotype ♂, **Burma**: Tenasserim Valley (*Doherty*) (BMNH).

Paratypes. 2 ♂, data as holotype (BMNH).



Figs 54–60 *Amphipsyche exsiliens* ♂. 54, wing venation; 55, legs; 56, maxillary palp; 57, genitalia, lateral view; 58, genitalia, ventral view; 59, phallotheca, lateral view; 60, phallotheca with endotheca everted.

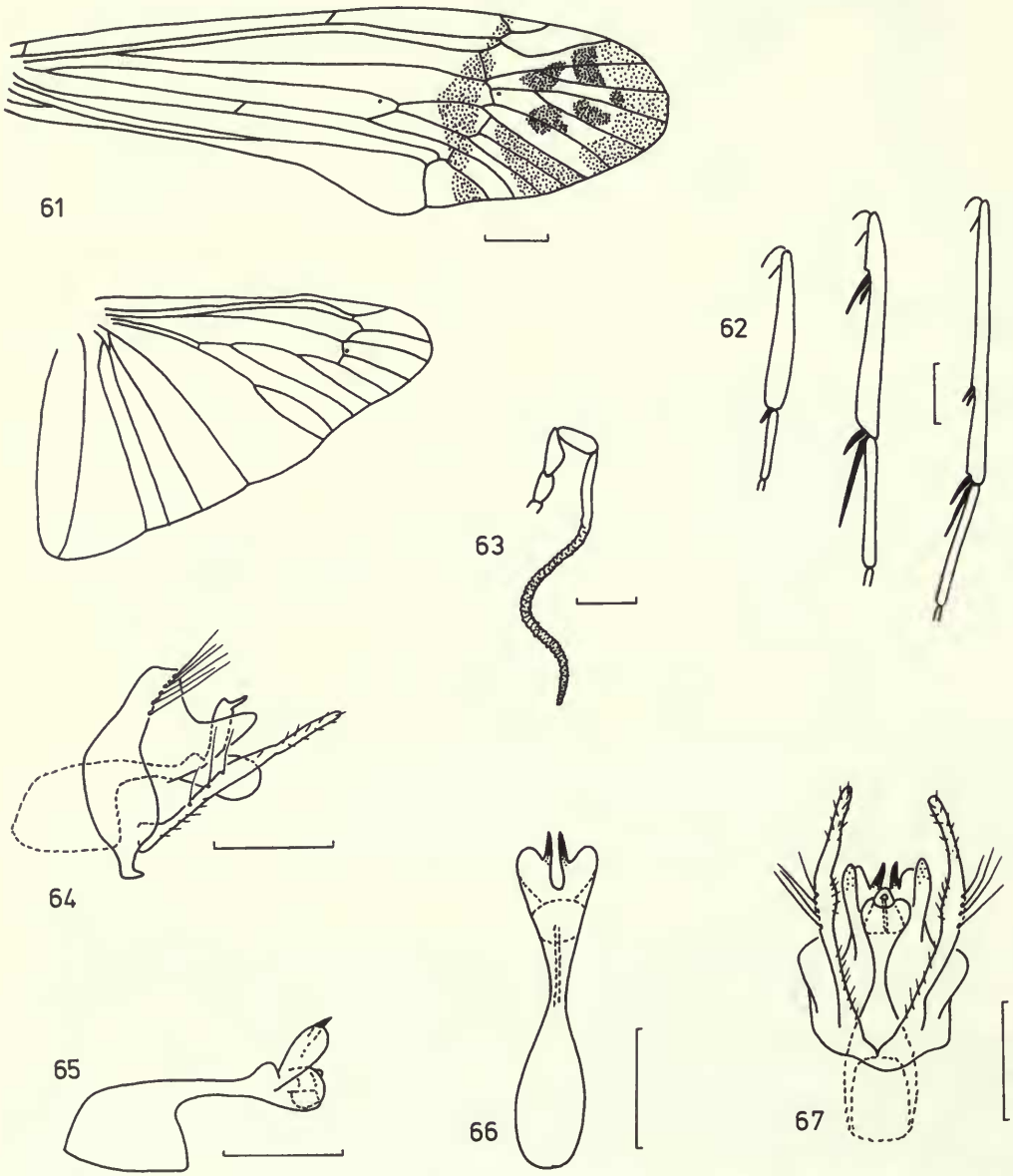
Amphipsyche gratiosa Navás

(Figs 61–67)

Amphipsyche gratiosa Navás, 1922: 62. Holotype ♂, VIETNAM: Tonkin, Hag Song, vii.1918 (lost).

♂. Antenna 25 mm, with *c.* 85 segments. Fore wing 10–12 mm. Body yellowish brown, antennal segments narrowly annulated with brown. Fore wing pale yellow with striking pattern; pale brown streak across whole width of wing proximal to anastomosis; five dark brown spots in apical area, partially linked to pale brown areas in apical forks; venation as in Fig. 61. Spurs 1.4.4 (Fig. 62). Maxillary palp 5-segmented, 5th segment secondarily annulated, much longer than segments 1–4 combined (Fig. 63).

♀. Unknown.



Figs 61–67 *Amphipsyche gratiosa* ♂. 61, wing venation; 62, legs; 63, maxillary palp; 64, genitalia, lateral view; 65, phallotheca, lateral view; 66, phallotheca, dorsal view; 67, genitalia, ventral view.

GENITALIA ♂ (Figs 64–67). Ninth segment relatively narrow laterally. Base of phallotheca elongate, flattened; stem narrow; apex with pair of leaf-like lobes, each bearing single spine on inner surface; pointed dorsal lobe proximal to these apical lobes. Inferior appendage slender; setigerous projection midway on inner surface in ventral view; terminal segment not differentiated.

REMARKS. This species is easily recognized by its prominent wing pattern. The unusual genitalia are also diagnostic, and suggest no close affinities with the other species in the *apicalis*-group. I have assumed that the dorsal lobes are not modified endothecal spines, despite their superficial similarity to those structures, because no other species in the genus has spines with lobate bases. There is certainly a close superficial similarity between the phallotheca of this species and that of *meridiana* for example, although all other critical characters of this species definitely place it in the *apicalis*-group. One male examined has a 'false' discoidal cell in the left fore wing only, a character otherwise seen only in *apicalis*.

The type of this species should be in the Navás collection (now in Barcelona) but is apparently missing (T. R. New, pers. comm.); however the species is easily recognizable from Navás's figure. In addition to the distribution records below, the type was collected in Vietnam.

MATERIAL EXAMINED

4 ♂, **Burma, Thailand** (BMNH).

Amphipsyche petiolata Ulmer

(Figs 68–77)

[*Amphipsyche proluta* McLachlan; Ulmer, 1910: 55; 1913: 79. Misidentifications.]

Amphipsyche petiolata Ulmer, 1930: 434. Lectotype ♀ [listed as 'holotype' by Weidner, 1964: 67], JAVA (ZM), designated by Ulmer, 1951: 197 [examined].

Amphipsyche minima Banks, 1931: 395. LECTOTYPE ♀, WEST MALAYSIA (BMNH), here designated [examined]. **Syn. n.**

Amphipsyche pubescens Kimmins, 1955: 387. Holotype ♂, BORNEO (BMNH) [examined]. **Syn. n.**

♂. Antenna *c.* 35 mm, with *c.* 80 segments. Fore wing 9–11 mm. Body yellowish brown; posterior part of vertex and dorsal surface of mesothorax brown. Antenna pale yellow, annulated with brown, segments becoming more fuscous towards apex. Fore wing pale golden yellow, with pale brown apex, brownish stripe across anastomosis and dark brown spot in fork I; venation as in Fig. 68. Spurs 1.4.4 (Fig. 69). Maxillary palp 5-segmented, 5th segment secondarily annulated, about three times length of segments 1–4 combined (Fig. 70).

♀. Antenna 10 mm, with *c.* 45 segments. Fore wing 7–8 mm. General coloration as in ♂. Fore wing very pale yellow, pale brown stripe across anastomosis, sometimes slight brown marking in fork I; venation as in Fig. 74. Spurs 1.4.4 (Fig. 75). Maxillary palp 5-segmented, 5th segment secondarily annulated, about twice length of segments 1–4 combined (Fig. 77).

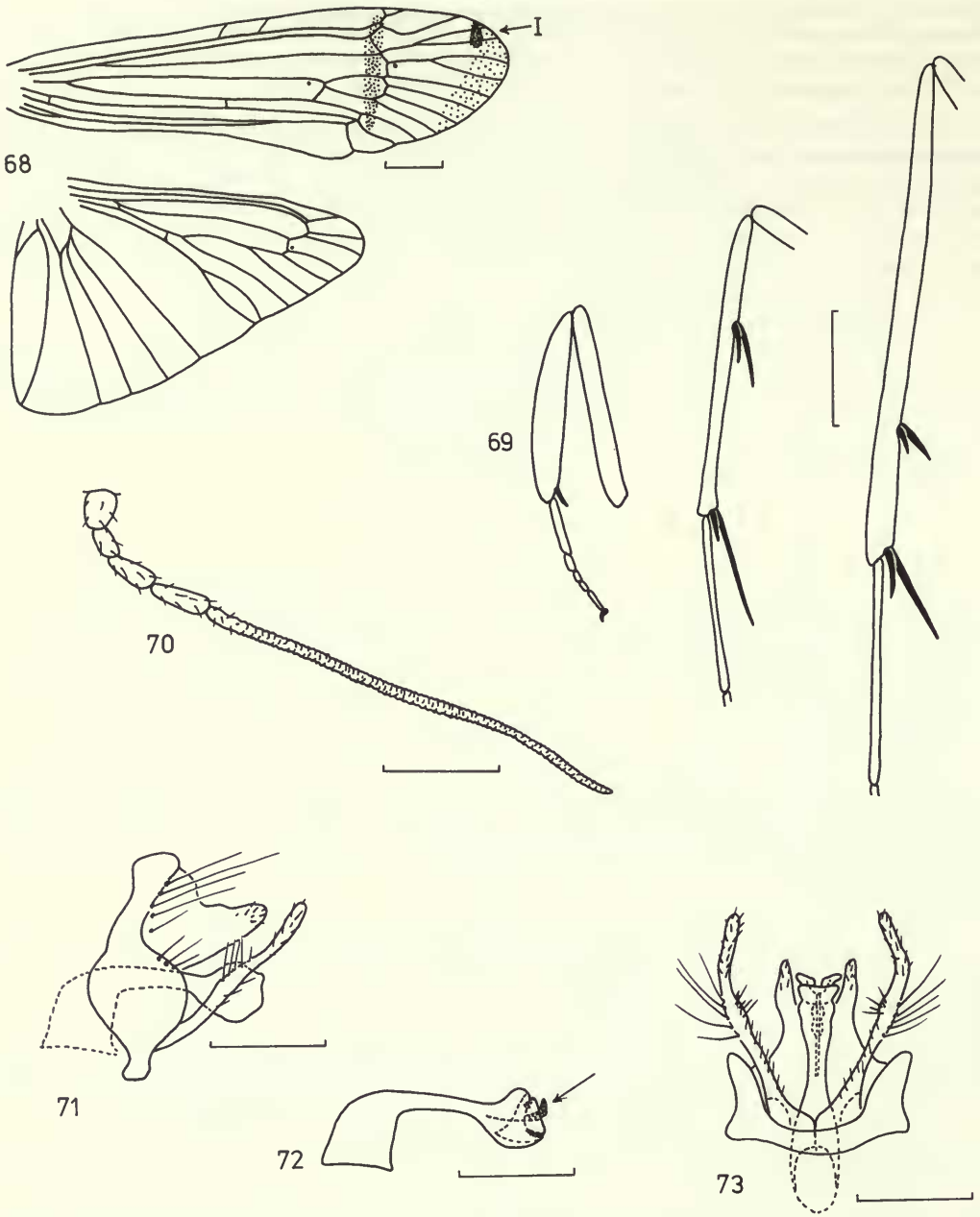
GENITALIA ♂ (Figs 71–73). Ninth segment broadly rounded laterally. Base of phallotheca narrow, rectangular, narrow stem abruptly right-angled. Tip of phallotheca globose with bifurcate membranous process arising from apical depression, abruptly up-turned at apex (Fig. 72). Inferior appendage narrow with setigerous median projection on inner surface, terminal segment not differentiated.

GENITALIA ♀ (Fig. 76). Eighth sternites narrow, inner thickened edges slightly incurved; posterior margin produced as rounded point.

REMARKS. The male of this species can be distinguished from others in the *apicalis*-group by the form of the phallotheca. The apical rod-like process superficially resembles an endothecal spine but it is a membranous median structure. Within this species-group the only other known female is that of *apicalis*, which has differently shaped eighth sternites and a short apical segment of the maxillary palp.

I have taken Ulmer's subsequent (1951) listing of the Javan syntype as 'type' as a lectotype designation. Weidner (1964) listed this specimen as the holotype, but this is incorrect as Ulmer's original description was based on three syntypes.

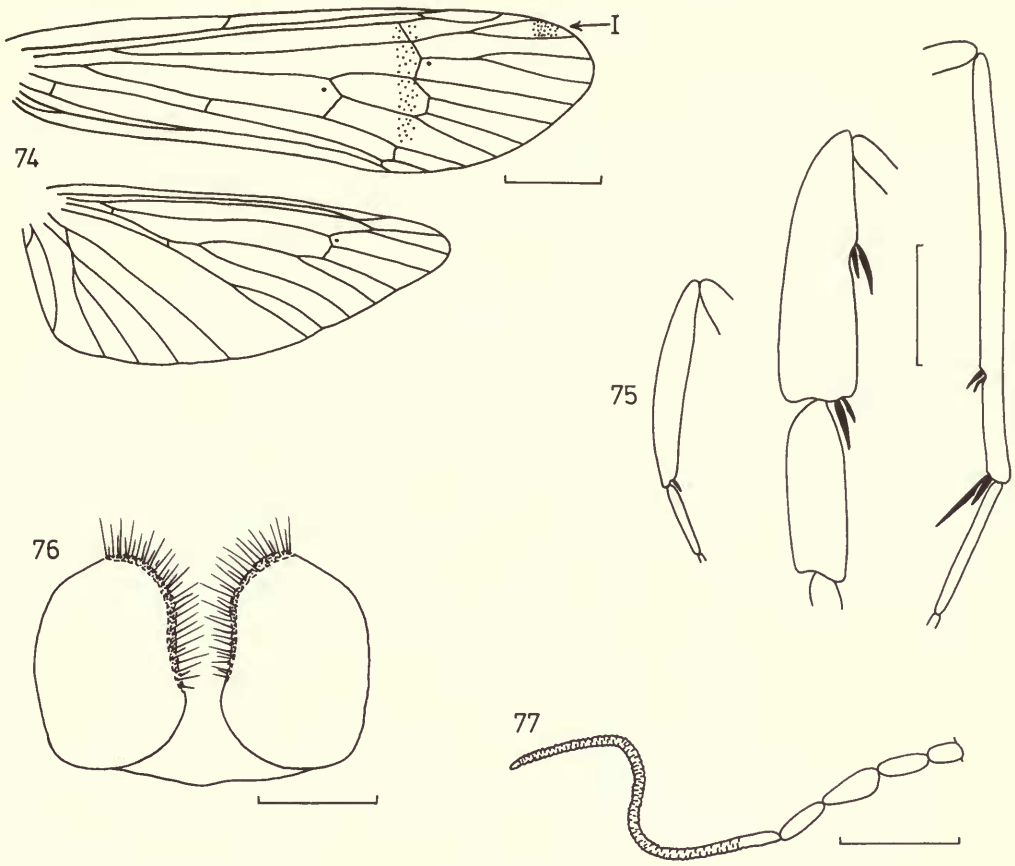
It is not clear from Banks's (1931) description of *minima* how many specimens constituted the type-series. Of the two extant syntypes (with identical data, and both labelled 'type' by Banks)



Figs 68–73 *Amphipsyche petiolata* ♂. 68, wing venation; 69, legs; 70, maxillary palp; 71, genitalia, lateral view; 72, phallotheca, lateral view; 73, genitalia, ventral view.

the MCZ specimen was labelled 'paratype' by H. H. Ross in 1965. I have therefore designated the BMNH syntype as lectotype. Ulmer (1951) remarked on the similarity of *minima* to *petiolata*.

Mosely identified the type-material of *pubescens* as *petiolata*, but Kimmins decided that it represented a distinct species on the grounds that Ulmer had not mentioned an apical wing spot



Figs 74–77 *Amphipsyche petiolata* ♀. 74. wing venation; 75, legs; 76, eighth sternites; 77, maxillary palp.

in the description of *petiolata*. However, Ulmer's species was described from females only, and the wing markings are very faint in this sex.

In addition to the distribution records below, Ulmer (1930) also recorded this species from Sumatra.

MATERIAL EXAMINED

Lectotype ♀ of *petiolata*, **Java**: Wonosobo, iv.1909 (*Jacobson*) (ZM). Lectotype ♀ of *minima*, **West Malaysia**: Kedah, nr Jitra, catchment area, 9.iv.1928 (*Pendlebury*) (BMNH). Holotype ♂ of *pubescens*, **Borneo**: Sarawak, foot of Mt Dulit, junction of Rivers Tinjar and Lejok, 20.viii.1932 (*Hobby & Moore*) (BMNH).

3 ♂, 5 ♀, **West Malaysia** (1 ♀ paralectotype of *minima*); **Borneo**: Sarawak (1 ♂, 2 ♀ paratypes of *pubescens*) (BMNH, MCZ).

The *meridiana*-group

Genae rounded, with no pubescence. Fork II sessile in fore wing. 0 spurs on fore leg; mid spurs sometimes reduced to 3 or 2; hind spurs always reduced to 3 or 2. Fifth segment of maxillary palp often reduced, or fused with 4th segment. ♂ inferior appendages slender; phallocrypt pocket and pre-anal appendages absent. Phallotheca with up to three pairs of endothecal spines. Ninth segment with single (dorsal) row of setae in lateral view.

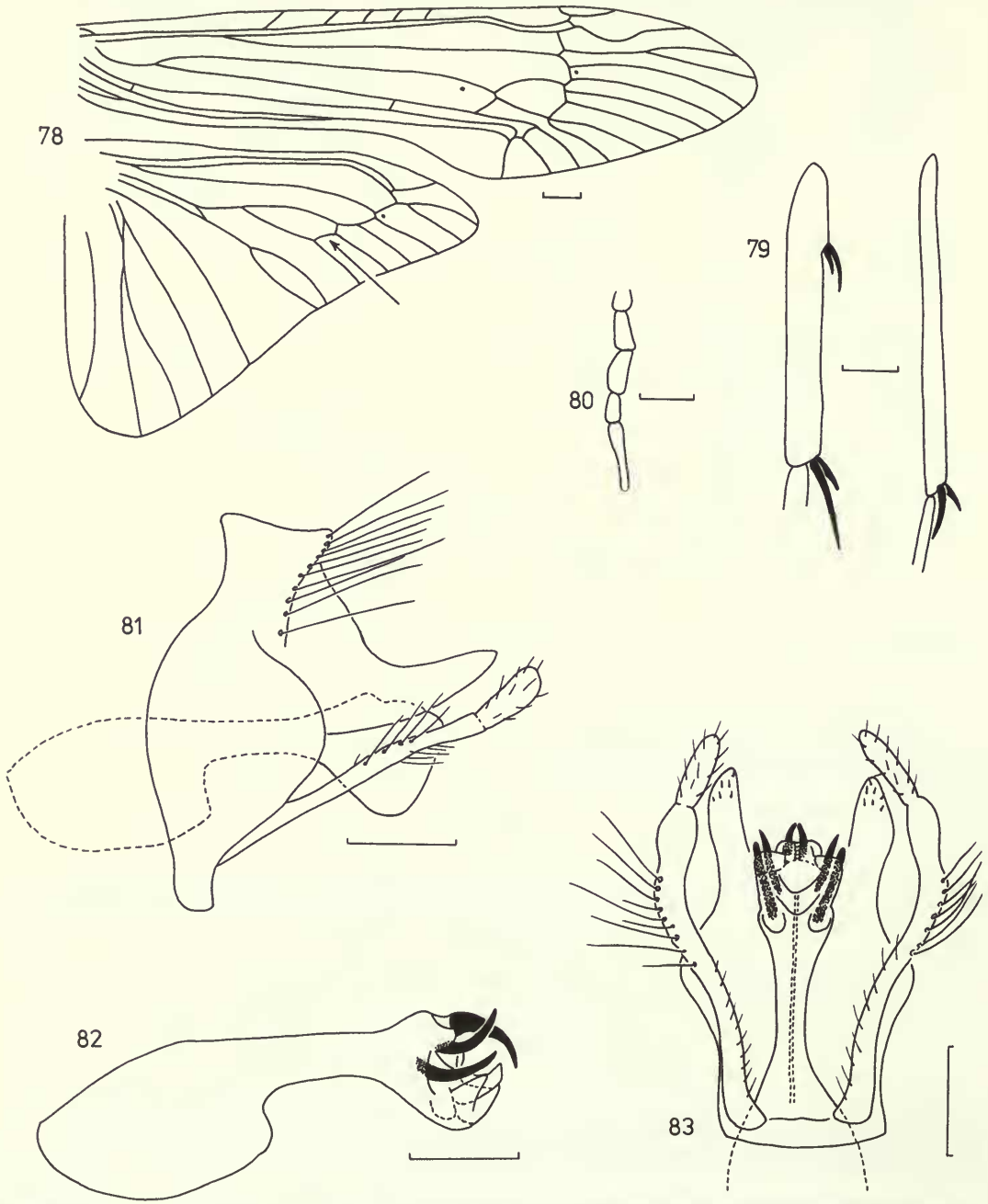
Africa, Madagascar, India, Sri Lanka, Nepal, Cambodia, West Malaysia, Sumatra, Java, Borneo, Philippines.

Amphipsyche magna Banks

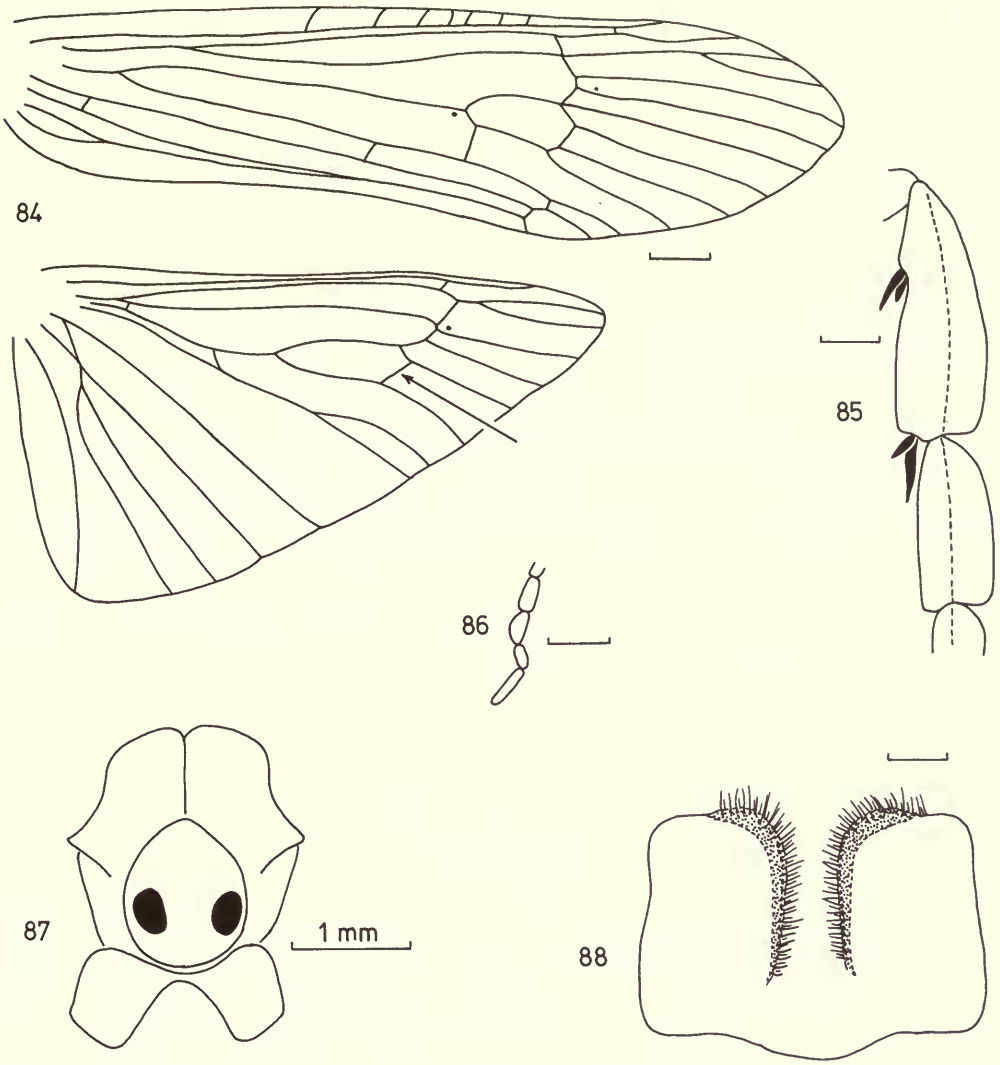
(Figs 78–88)

Amphipsyche magna Banks, 1939: 58. Holotype ♂, PHILIPPINES (MCZ) [examined].

♂ (holotype only). Antennae missing, described by Banks (1939) as 'pale, tips of joints dark'. Fore wing 20mm. Head, thorax and abdomen pale yellowish brown, mesoscutellum with two round dark brown



Figs 78–83 *Amphipsyche magna* ♂. 78, wing venation; 79, mid and hind tibiae; 80, maxillary palp; 81, genitalia, lateral view; 82, phallotheca, lateral view; 83, genitalia, ventral view.



Figs 84–88 *Amphipsyche magna*. 84. ♀ wing venation; 85, ♀ mid tibia, 86, ♀ maxillary palp; 87, ♂ thorax, dorsal view; 88, ♀ eighth sternites.

markings (Fig. 87). Fore wing elongate, yellowish brown with no markings. Venation as in Fig. 78; closed median cell in hind wing formed by M_2–M_{3+4} cross-vein. Spurs 0.4.2 (Fig. 79), not 1.4.2 as stated by Banks. Maxillary palp 5-segmented, 5th segment short, not secondarily annulated (Fig. 80).

♀ (single example). Antennal length unknown (specimen damaged). Fore wing 15 mm. Coloration as in ♂, with similar round markings on mesoscutellum. Basal antennal segments pale yellow, narrowly annulated with brown. Venation as in Fig. 84; closed median cell in hind wing as in ♂. Spurs 0.4. [? 2] (hind legs missing) (Fig. 85). Maxillary palp 5-segmented, 5th segment shorter than in ♂ (Fig. 86).

Genitalia ♂ (Figs 81–83). Ninth segment broadly rounded laterally. Base of phallotheca strongly flattened dorso-ventrally, apex rounded. Three pairs of endothecal spines present; dorsal pair directed ventrally, mid and ventral pairs curved dorsally. Inferior appendage thin and strongly sinuous; terminal segment moderately clearly differentiated.

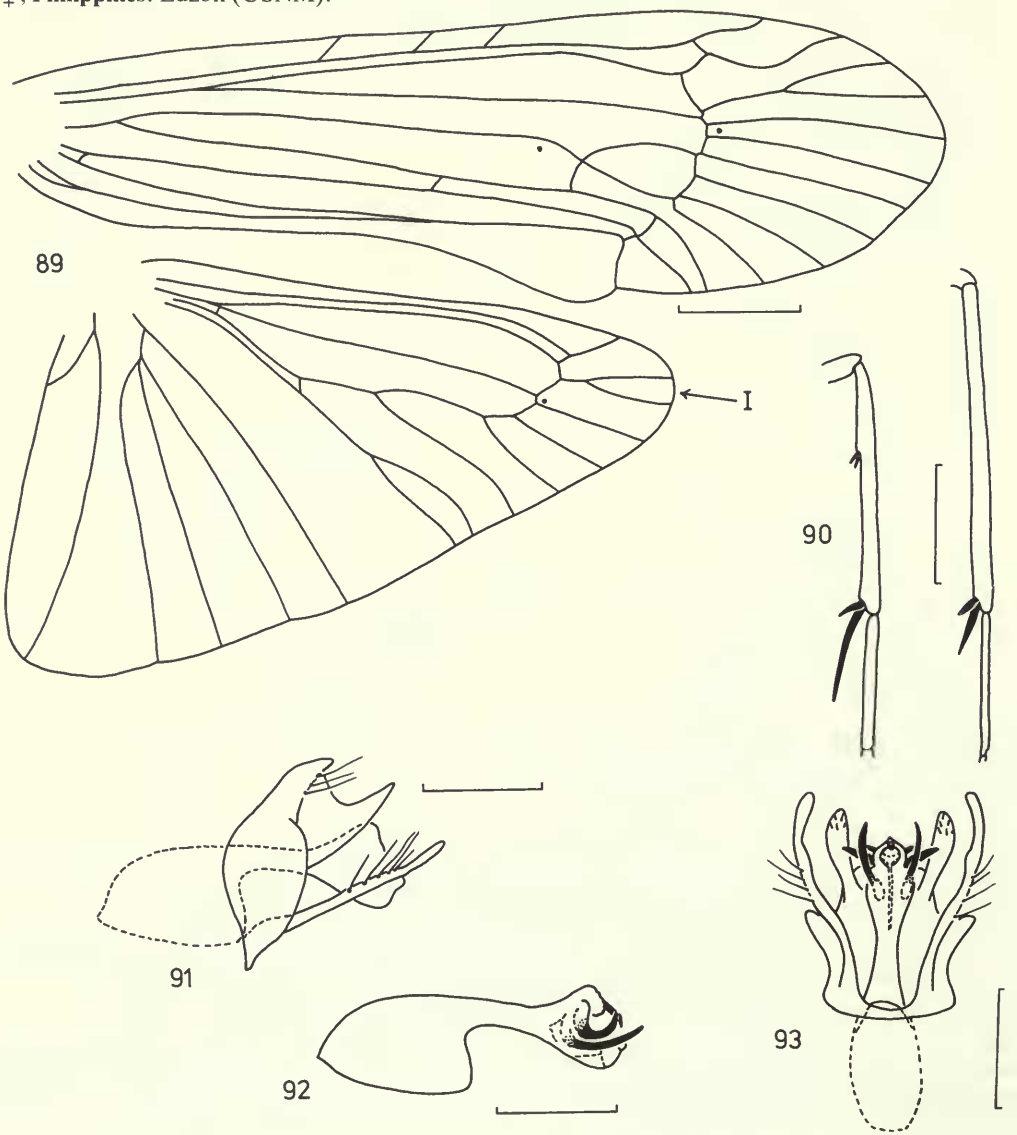
Genitalia ♀ (Fig. 88). Eighth sternites subrectangular, much longer than broad; inner thickened margins broad.

REMARKS. Despite the unlikely sounding combination of names, it seems that *magna*, the largest species in the genus, and *parva*, one of the smallest, are sister species. They are, of course, easily separable by the great disparity in size, and *magna* is particularly easy to recognize by the mesoscutellar markings and hind wing median cell in both sexes. Both *magna* and *parva* have the full complement of three pairs of endothecal spines and both have the unusually shaped phallothecal base, which is elongate and strongly flattened in lateral view.

This is the first description of the female of *magna*. The two striking external characters of the species, the mesoscutellar markings and the hind wing median cell, are the same in each sex, as is the reduced condition of the maxillary palps.

MATERIAL EXAMINED

Holotype ♂, **Philippines**: Luzon, Del Carmen, 15.xi.1927 (*Uichanco*) (type no. 23471, MCZ).
1 ♀, **Philippines**: Luzon (USNM).



Figs 89–93 *Amphipsyche parva* ♂. 89, wing venation; 90, mid and hind tibiae; 91, genitalia, lateral view; 92, phallotheca, lateral view; 93, genitalia, ventral view.

Amphipsyche parva Banks

(Figs 89–93)

Amphipsyche parva Banks, 1920: 354. Holotype ♂, BORNEO (MCZ) [examined].

♂ (holotype only). Antenna *c.* 25 mm with *c.* 80 segments. Fore wing 8 mm. Antennal segments pale yellow, slightly annulated with brown. Head, thorax and abdomen yellowish brown. Fore wing very pale yellow, almost colourless, with no markings. Venation as in Fig. 89: R_1 in fore wing strongly sinuous, fork I in hind wing clearly stalked. Spurs 0.4.2 (Fig. 90). Maxillary palps missing.

♀. Unknown.

GENITALIA ♂ (Figs 91–93). Ninth segment only slightly broadened laterally. Base of phallotheca strongly flattened dorso-ventrally, apex rounded. Three pairs of endothecal spines present; dorsal pair short, curved latero-ventrally; mid pair strongly curved dorsally; ventral pair long and almost straight, slightly directed dorsally. Inferior appendage thin and sinuous, terminal segment scarcely differentiated.

REMARKS. *A. parva* and *magna* are the only two species in the genus to possess three pairs of endothecal spines. *A. parva* is easily distinguished from *magna* (its sister species) by its small size and lack of thoracic markings. Little can be surmised about the maxillary palps of this species (which are missing in the holotype): although these are often reduced in the *meridiana*-group, this is not invariably the case, and the shortened apical segment in the sister species *magna* may be a unique character within this species-pair.

MATERIAL EXAMINED

Holotype ♂, **Borneo**: Mindai, vi.1882 (*Grabowsky*) (type no. 10886, MCZ).

Amphipsyche sinhala sp. n.

(Figs 94–103)

♂. Antenna *c.* 35 mm, with *c.* 85 segments. Fore wing 10–12 mm. Body pale yellowish brown; basal antennal segments narrowly annulated with pale brown, apical segments fuscous. Fore wing very pale yellow with no markings; venation as in Fig.94. Spurs 0.4.2 (Fig. 95). Maxillary palp 5-segmented; 5th segment secondarily annulated, approximately equal in length to segments 1–4 combined (Fig. 96).

♀. Antenna *c.* 14 mm, with *c.* 65 segments. Fore wing 7–8 mm. Coloration as in ♂. Venation as in Fig. 100. Spurs 0.4.2 (Fig. 101). Maxillary palp as in ♂, but 5th segment slightly shorter than segments 1–4 combined (Fig. 103).

GENITALIA ♂ (Figs 97–99). Ninth segment broad laterally. Phallotheca with moderately narrow stem, broadly truncate at apex. Mid endothecal spines very short, rod-like (Fig. 98); dorsal and ventral endothecal spines absent. Inferior appendage moderately narrow, slightly sinuous; terminal segment clearly differentiated.

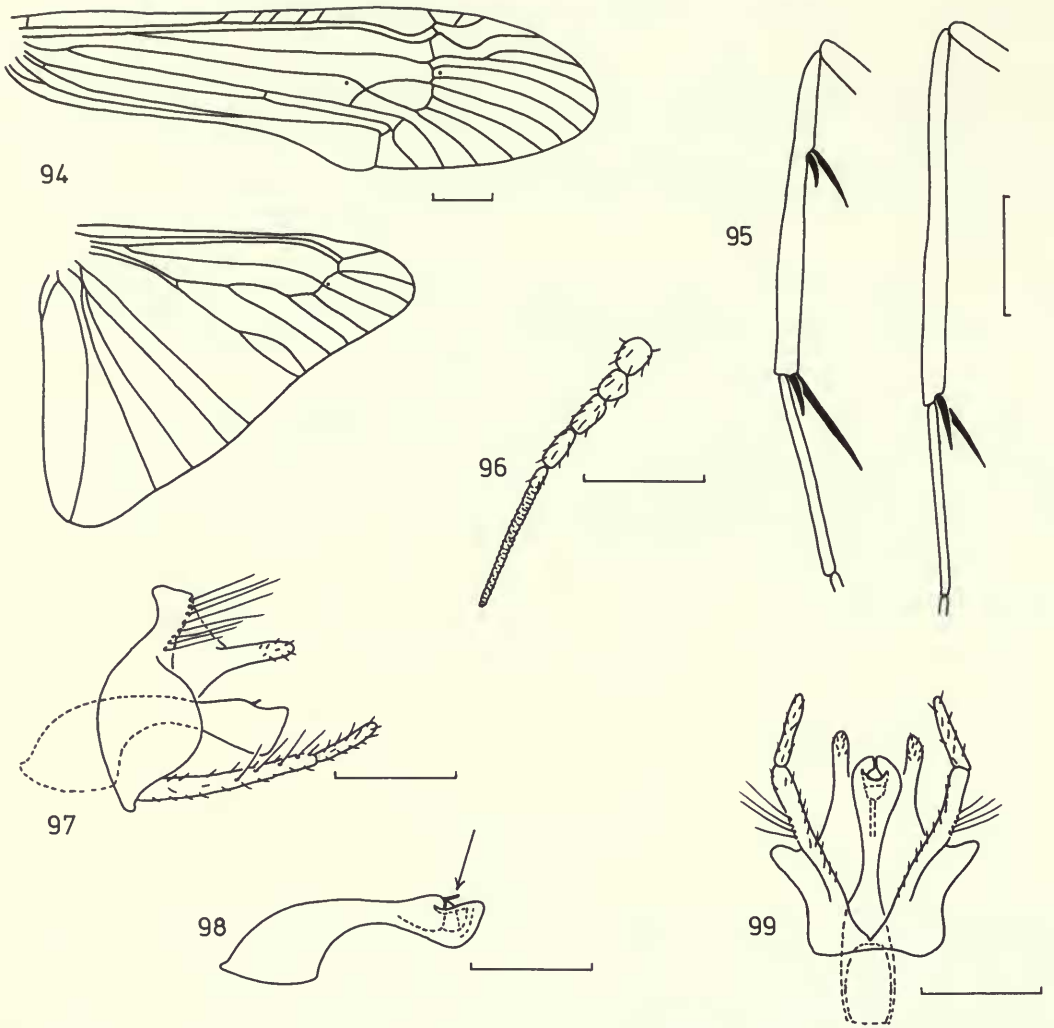
GENITALIA ♀ (Fig. 102). Eighth sternites narrow, outer borders strongly sloping, posterior border broadly pointed.

REMARKS. *A. sinhala* is apparently restricted to Sri Lanka, and the only other species reported from that country is *meridiana*. They can be separated easily on genitalic differences in both sexes, as well as on the spur formula; *meridiana* always has at least three spurs on the hind tibia in both sexes. Moreover, there is little overlap in size, *sinhala* being a noticeably small species. *A. sinhala* also resembles *bengalensis*, but is distinguished by the much shorter endothecal spines.

MATERIAL EXAMINED

Holotype ♂, **Sri Lanka**: Panamure, 15–21.x.1970 (*Flint*) (USNM).

Paratypes. **Sri Lanka**: 16 ♂, 36 ♀, data as holotype (all in USNM except 2 ♂, 2 ♀ in BMNH); 2 ♂, 18 ♀, Sella Kataragama, Menik Ganga, 24.x.1970 (*Flint*) (USNM).

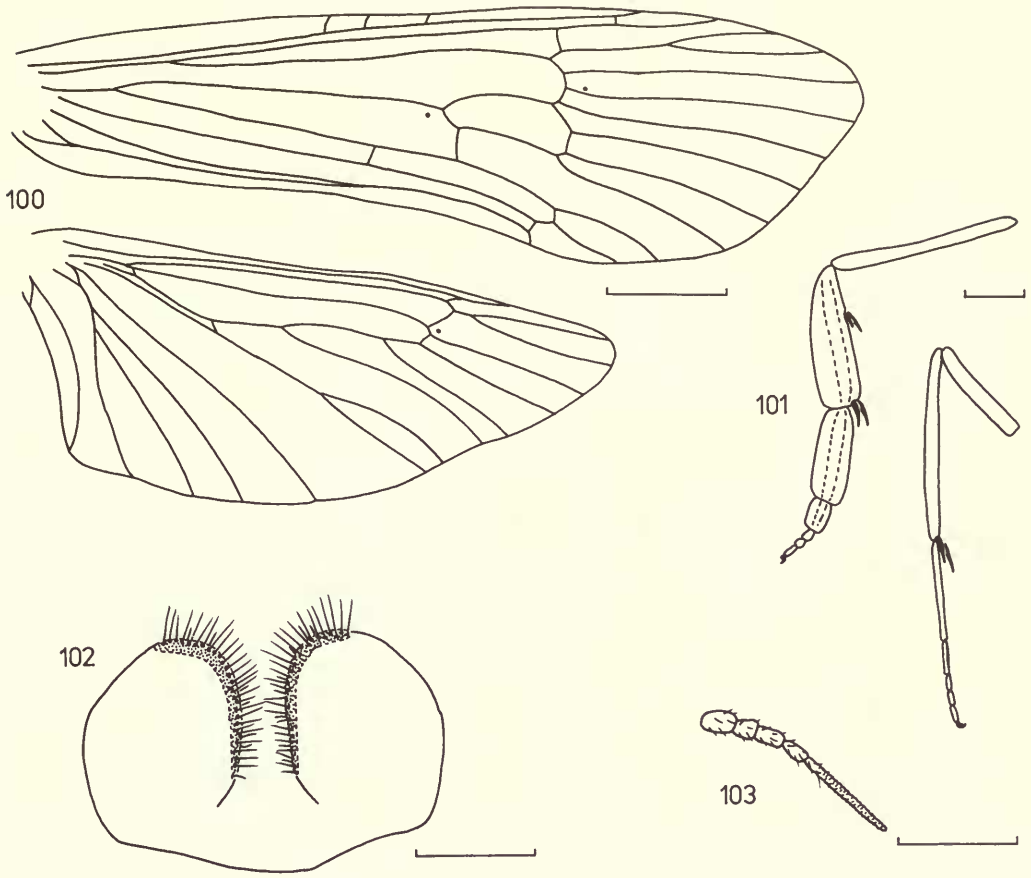


Figs 94–99 *Amphipsyche sinhala* ♂. 94, wing venation; 95, mid and hind tibiae; 96, maxillary palp; 97, genitalia, lateral view; 98, phallotheca, lateral view; 99, genitalia, ventral view.

Amphipsyche meridiana Ulmer

(Figs 104–114)

Amphipsyche meridiana Ulmer, 1909: 134. LECTOTYPE ♀, JAVA (RNH), here designated [examined].
[*Phanostoma* sp. Betten, 1909: 234.]
Amphipsyche nirvana Banks, 1913: 236. Holotype ♂, INDIA (MCZ) [examined]. **Syn. n.**
Amphipsyche vedana Banks, 1913: 235. Holotype ♀, INDIA (MCZ) [examined]. **Syn. n.**
Ampsipsyche [sic] *propinqua* Ulmer, 1927: 177. LECTOTYPE ♂, CAMBODIA (MNHU), here designated [examined]. **Syn. n.**
[*Amphipsyche proluta* McLachlan; Navás, 1931*b*: 91; 1934: 227. Misidentifications.]
Amphipsyche indica Martynov, 1935: 199. 8 syntypes, INDIA: 1 ♂, Bihar, Mokameh, at light; 1 ♂, Bihar, Dinapore, at light (*Annandale*); 2 ♂, 2 ♀, Bihar, Pusa, 5–10.xi.1915 (*Gravely*); 2 ♂, E. Bengal, Damukdia Ghat, at light on board steamer, 30.vi.1908 (2 syntypes in ZSI, the other 6 lost) [not examined]. **Syn. n.**



Figs 100–103 *Amphipsyche sinhala* ♀. 100, wing venation; 101, mid and hind legs; 102, eighth sternites; 103, maxillary palp.

Amphipsyche tricalcarata Martynov, 1935: 197. Holotype ♀, India: Orissa, Puri district, Bhubaneswar, 4–6.xi.1912 (*Gravely*) (lost from ZSI). [Synonymized with *indica* by Schmid, 1958: 107.]

Amphipsyche sigmosa Navás, 1935: 105. LECTOTYPE ♂, India (MNHN), here designated [examined]. **Syn. n.**

♂. Antenna *c.* 40 mm with up to 100 segments. Fore wing 13–15 mm. Body pale yellowish brown, antennal segments pale golden brown. Fore wing pale golden yellow, sometimes with pale brown marking behind R_1–*Rs* cross-vein. Venation as in Fig. 105; R_1 in fore wing strongly sinuous both proximal and distal to anastomosis. Spurs 0.4.3 or 0.4.4 (pre-apical spurs on hind tibia always very small) (Fig. 106). Maxillary palp 5-segmented, 5th segment secondarily annulated, approximately equal in length to segments 1–4 combined (Fig. 107).

♀. Antenna *c.* 18 mm, with *c.* 70 segments. Fore wing 8–12 mm. Coloration as in ♂; dark marking on fore wing always absent. Venation as in Fig. 111; fork IV in fore wing occasionally stalked. Spurs (Fig. 112) and maxillary palp (Fig. 114) as in ♂.

Genitalia ♂ (Figs 104, 108–109). Ninth segment moderately broad laterally. Phallotheca elongate, with narrow stem. Dorsal endothecal spines absent, in their place a pair of semi-membranous leaf-like lobes, variable in shape (Fig. 109). Mid and ventral endothecal spines short, varying in relative length; ventral pair occasionally lost. Inferior appendage narrow and sinuous, terminal segment moderately well differentiated.

Genitalia ♀ (Fig. 113). Eighth sternites broad and squarish with broadly rounded corners.

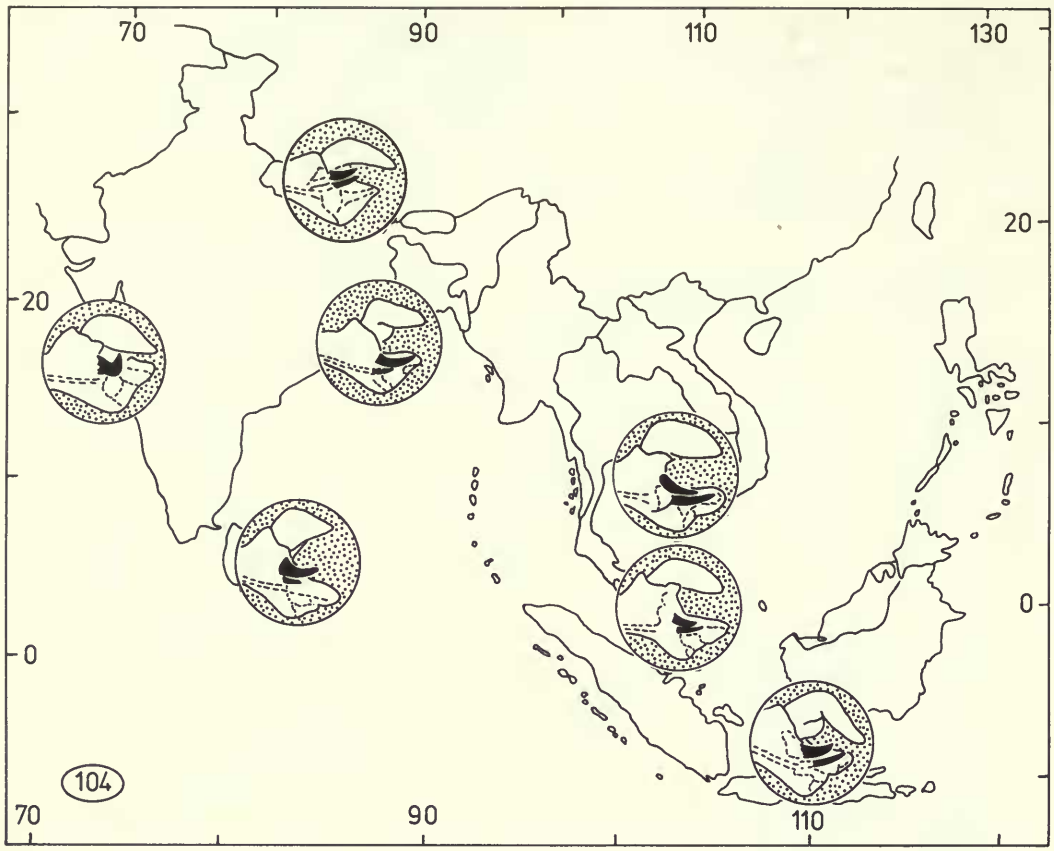
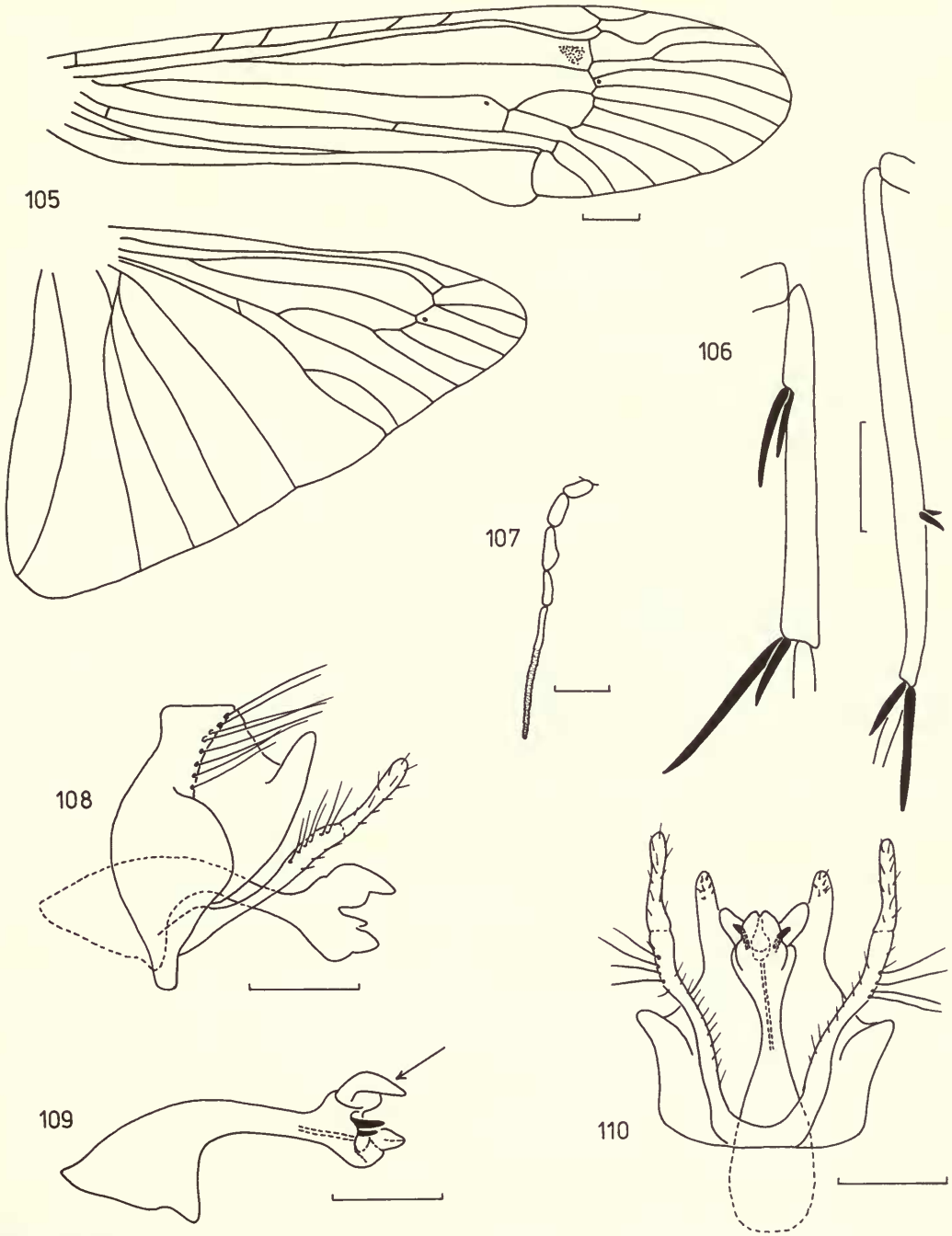


Fig. 104 Variation in ♂ genitalia of *Amphipsyche meridiana* throughout its range.

Remarks. *A. meridiana* is the most common and widespread of the Asian species in the genus. The male is easily recognized by the dorsal leaf-like lobes on the phallotheca, but the female may be confused with *sinhala* unless it is examined closely; the hind pre-apical spurs are always extremely small, thus the spur formula may be taken erroneously as 0.4.2.

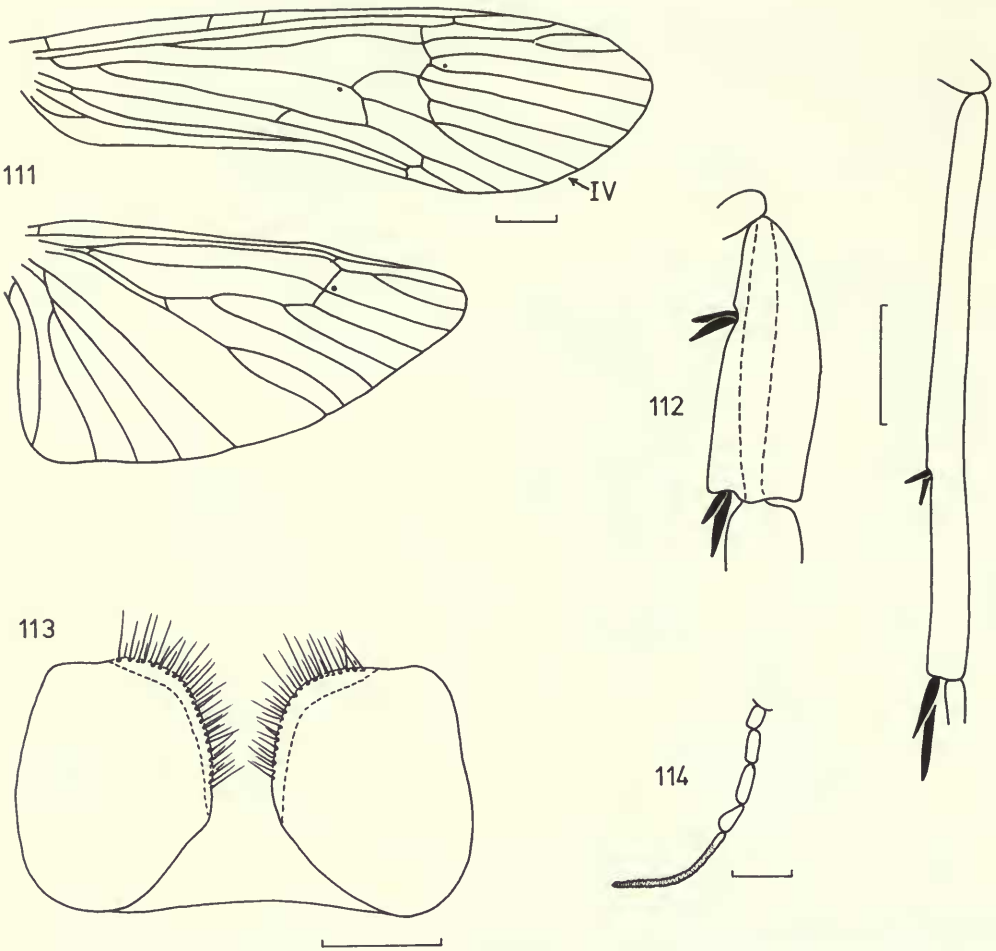
The large number of synonyms of this species is partly a result of its morphological variability over a wide geographical range. Banks (1913) said that Betten's (1909) '*Phanostoma* sp.' was the same as, or very similar to, *nirvana*, and Martynov (1935) said that it was identical with his new species *indica*. Banks (1939) apparently regarded *indica* as a synonym of *nirvana*, as he placed the name *indica* in parentheses after *nirvana*. Meanwhile, Ulmer (1927) had compared *propinqua* with *nirvana* (but not with his own species *meridiana*) but later (1951) noted that *nirvana*, *propinqua* and *meridiana* were all very similar. Thus the Indian species were long considered as being synonymous, but the synonymy with *meridiana* was not suspected, partly because of the geographical separation (*meridiana* being described from Java) and partly because the male of *meridiana* was not described until 1951.

The extent of variation in the male phallotheca is shown semi-diagrammatically in Fig. 104. The mid endothecal spines are moderately consistent in size and form throughout the whole range, although in the single known male from Bombay they are very short and broad, and bent abruptly upwards. However, the ventral endothecal spines vary greatly, and there seems to be a correlation with distribution, such that in the most eastern specimens they are much longer than the mid spines, whereas in the western (Indian) populations they are usually much shorter, and even lost in specimens from west India (and also occasionally Sri Lanka). There is in fact a discontinuity in the distribution of this species, with no specimens known from countries



Figs 105–110 *Amphipsyche meridiana* ♂. 105, wing venation; 106, mid and hind tibiae; 107, maxillary palp; 108, genitalia, lateral view; 109, phallotheca, lateral view; 110, genitalia, ventral view.

between India and Cambodia. There may be justification for considering the two populations as subspecifically distinct, in which case the Indian subspecies would have to be named *meridiana nirvana*, with the nominate subspecies in South East Asia, but I do not propose such a formal division at present.



Figs 111–114 *Amphipsyche meridiana* ♀. 111, wing venation; 112, mid and hind tibiae; 113, eighth sternites; 114, maxillary palp.

I do not believe that the 'paratype' of *meridiana* mentioned by Weidner (1964) has any type-status. Although from the type-locality, it bears a printed label with the date 'Dec. 1908'. A 'Paratype' label has also been attached, bearing the hand-written date '8.1907', not in Ulmer's hand, to conform to the published type-data. However, the other labels do not match those on the two remaining syntypes in Leiden; of the original three syntypes mentioned by Ulmer in the RNH, one has apparently been lost (Geijskes, *in litt.*).

Of the three syntypes of *propinqua* described by Ulmer (1927) I have examined the two males in MNHU and designate as lectotype the one labelled 'type' by Ulmer. The third male syntype, now a paralectotype (IP, not examined), lacks its abdomen (Director, IP, *in litt.*).

I was informed by Ghosh (*in litt.*) of the apparent loss of six syntypes of *indica*, and of the holotype of *tricalcarata* from the ZSI. The female syntypes of *sigmosa* (from Khandala) are also apparently lost, so the sole remaining male syntype in the MNHN is here designated as lectotype.

The larva of this species was described by Hafiz (1937, as *indica*), and by Ulmer (1957). There are some differences between these two descriptions, both in the gill formulae and in the head markings. Specimens from Java that I have examined differ slightly in gill counts from Ulmer's description, even though his material was also from Java (and Sumatra). Some aspects of the life

history are described by Seshadri (1955) and Boon (1979) – see p. 79. Some specimens in the BMNH, received via the Commonwealth Institute of Entomology, were captured on paddy-fields in India, but any economic significance of this is unknown.

MATERIAL EXAMINED

Lectotype ♀ of *meridiana*, **Java**: Batavia, viii.1907 (*Jacobson*) (RNH). Holotype ♂ of *nirvana*, **India**: Bengal, Pusa, at light, 23.iii.1908 (type no. 11755, MCZ). Holotype ♀ of *vedana*, **India**: Bengal, Pusa, 15.ix.1907 (type no. 11757, MCZ). Lectotype ♂ of *propinqua*, **Cambodia**: Mekong, Pnom-Pech, i.1914 (*Friederichs*) (MNHU). Lectotype ♂ of *sigmosa*, **India**: Bombay, Lonawla [= Lonavla, = Lonauli], 9.x.1934 (*Benavent*) (MNHN).

229 ♂, 332 ♀, *c.* 75 larvae, 2 pupae, **India**, **Sri Lanka**, **Nepal**, **Cambodia** (1 ♂ paralectotype of *propinqua*), **West Malaysia**, **Sumatra**, **Java** (1 ♀ paralectotype and 1 ♀ as 'paratype' of *meridiana*; see 'Remarks' above) (BMNH, MCZ, MNHU, RNH, USNM, ZM).

Amphipsyche bengalensis Martynov

(Figs 117, 118)

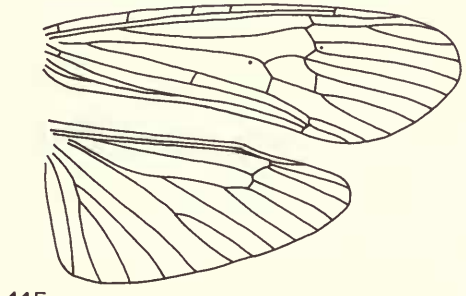
Amphipsyche bengalensis Martynov, 1935: 201. 2 ♂ syntypes, INDIA: Bengal, Calcutta, at light, 19.vi.1907 (*Hodgart*) (ZSI) [not examined].

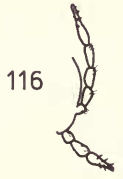
♂ (from Martynov, 1935). 'Body pale yellow. Antennae yellow, with narrow dark annulations. Anterior wings pale. R[R_1] curved in its apical portion even more strongly than in *A. indicum* [= *meridiana*] . . . In posterior wings first (apparently false) fork sessile, not pedicellate; . . . formula of spurs 1.4.2 [probably 0.4.2]. Length of body 6 mm.'

♀. Unknown.

GENITALIA ♂ (Figs 117, 118) (from Martynov, 1935). '10th [9th] segment as in [*meridiana*], but its side-lobes appear to be somewhat broader. Lower end-lobe of the penis [phallotheca] broader, distinctly excised in the middle and curved upwards (if seen from side); upper leaf-like lobes lacking, in their place is an oval elevation, behind which are situated two stick-shaped appendages [mid endothecal spines]; underside of the penis thickened before its lower end-lobe.'

REMARKS. This species seems to be most closely related to *sinhala*, but the male genitalia are different, assuming Martynov's figures to be accurate. Although Martynov gave no wing-length for *bengalensis*, this would also seem to be a larger species than *sinhala*, whose body length is





Figs 115–118 115, 116, *Amphipsyche extrema* ♀, (115) wing venation; (116) palps. 117, 118, *Amphipsyche bengalensis* ♂, (117) phallotheca, lateral view; (118), phallotheca, dorsal view. (After Martynov.)

only 4–5 mm. The 6 mm body length of *bengalensis* suggests that it is of a similar size to *meridiana*. The spur formula of this species should almost certainly be 0.4.2; Martynov probably mistook an apical seta on the fore tibia for a spur.

The two syntypes in the ZSI are damaged (Ghosh, *in litt.*) and I was unable to examine them. The species is known only from these two specimens from Bengal.

Amphipsyche extrema (Martynov) **comb. n.**

(Figs 115, 116)

Amphipsychella extrema Martynov, 1935: 202. 2 syntypes, INDIA: 1 ♀, Bengal, Calcutta, Eden Garden, at light, 26.v.1912 (*Gravely*); 1 ♀, Bengal, Calcutta, v.1915 (*Gravely*) (both lost from ZSI).

♂. Unknown.

♀ (from Martynov, 1935). 'Pale yellow. Antennae very slender, yellowish, with narrow darker annulations. Maxillary palpi very short, not reaching eyes; 2–4 joints subequal; 5th joint shorter than 3rd and 4th combined, its distal half slender and but very indistinctly annulated; labial palpi also very short [Fig. 116] . . . In anterior wings [Fig.115] three false veinlets are seen between C and Sc; 1st apical fork a little longer than its pedicel and somewhat approximated to R [R_1]; R long, slightly arcuate; . . . 4th apical fork with a short pedicel. RS_{1+2} in posterior wings simple, not united at its base with RS_3. Abdomen pale. Length of body 5·5 mm.' [From generic diagnosis of *Amphipsychella*] 'Spurs 0.2(1).2, the outer spur on the median legs reduced, indistinct.'

REMARKS. It is difficult to comment on the relationships of this species, as it is known only from the female which I have not examined; apparently both syntypes are lost from the ZSI (Ghosh, *in litt.*). However, the highly reduced spur formula, and the shortened maxillary palp place it in the *meridiana*-group. It would seem most closely related to *bengalensis, meridiana* and *sinhala*, but can be distinguished from these other Indian species by the spur formula and the maxillary palp.

Amphipsyche senegalensis (Brauer)

(Figs 120–129; distribution, Fig. 119)

Phanostoma senegalense Brauer, 1875: 71. Lectotype ♂, SENEGAL (NM), designated by Kimmins, 1962: 86 [examined].

Phanostoma curvinerve Navás, 1927: 214. LECTOTYPE ♀, EGYPT (USNM), here designated [examined]. **Syn. n.**

Amphipsyche senegalensis (Brauer) Kimmins, 1962: 85.

♂. Antenna *c.* 40 mm, with *c.* 75 segments. Fore wing 11–17 mm. Body pale yellowish brown, antenna narrowly annulated with brown. Fore wing pale yellow, often with brownish wedge-shaped pterostigmal marking; venation as in Fig. 120. Spurs 0.4.2 (Fig. 121). Maxillary palp 5-segmented; 5th segment secondarily annulated, slightly longer than segments 1 and 2 combined (Fig. 122).

♀. Antenna *c.* 15 mm, with *c.* 65 segments. Fore wing 9–12 mm. General coloration as in ♂. Fore wing usually unmarked, rarely with pale brown pterostigmal marking; venation as in Fig. 126; *Rs* in fore wing strongly sinuous. Spurs 0.2.2, 0.3.2 (Fig. 127) or 0.4.2. Maxillary palp similar to that of ♂; 5th segment approximately equal to 1 and 2 combined (Fig. 129).

GENITALIA ♂ (Figs 123–125). Ninth segment broadly rounded laterally. Base and stem of phallotheca narrow, apex bluntly rounded; no endothecal spines present. Inferior appendage slender; terminal segment moderately well differentiated.

GENITALIA ♀ (Fig. 128). Eighth sternites broadly rounded; slight indentation in middle of posterior edge, and outer posterior corners produced.

REMARKS. This species is easily distinguished from the other African species by the complete absence of endothecal spines in the male. The female can probably be distinguished by the very sinuous *Rs* in the fore wing, but this cannot be confirmed until the females of all the African species have been discovered. *A. senegalensis* has a very wide distribution, being found in virtually every country in the Afrotropical region except in the south-west and along the east

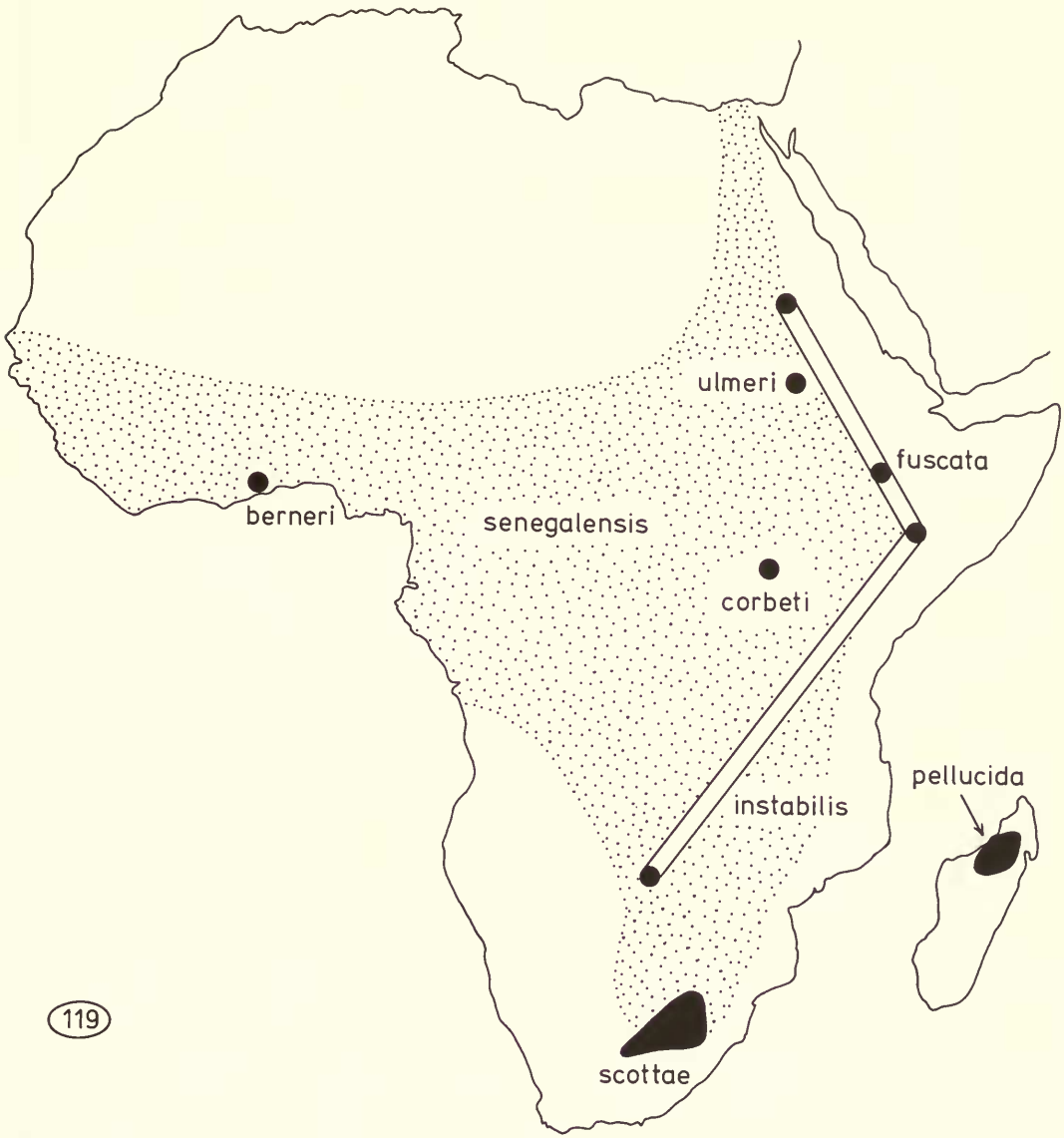


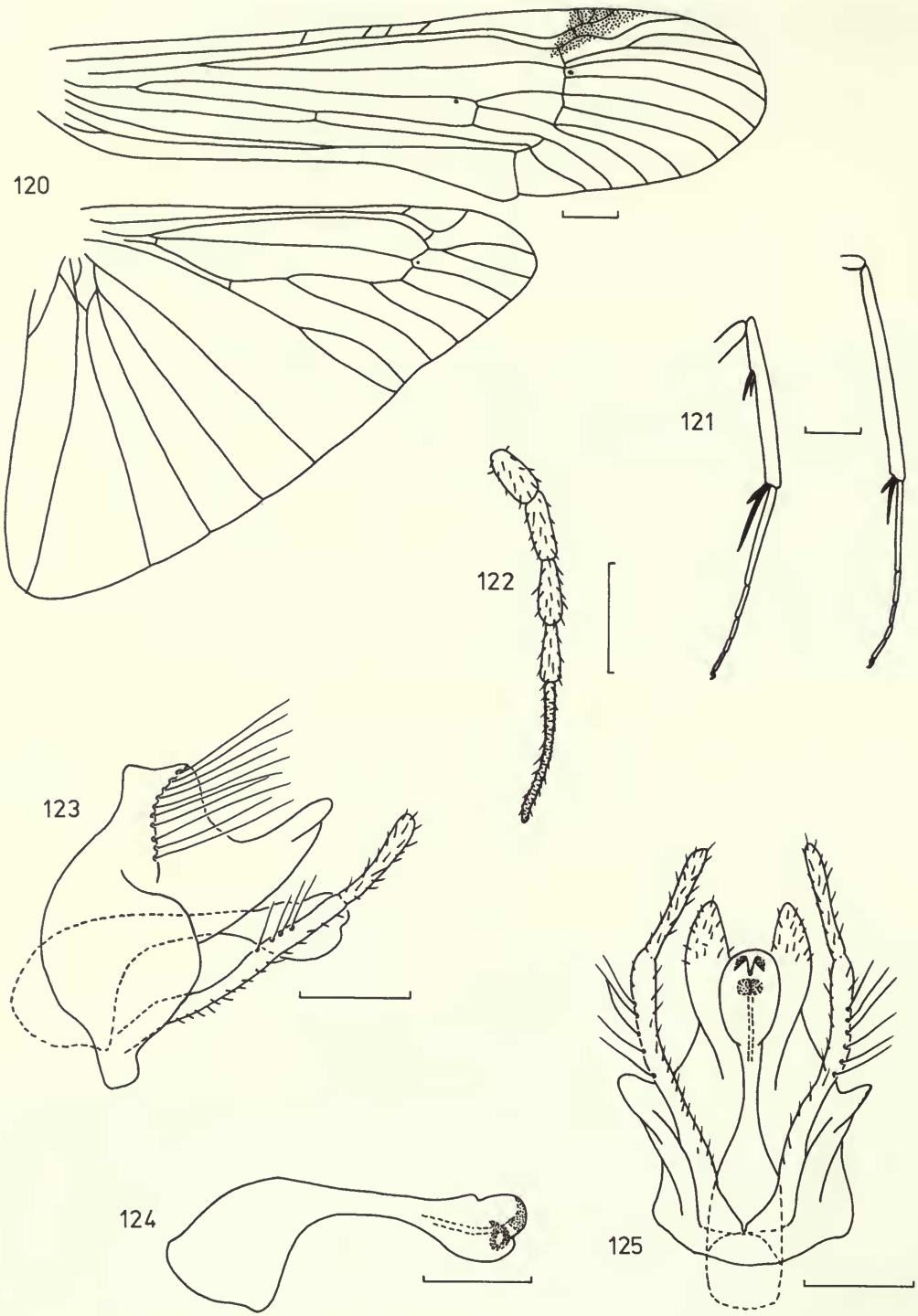
Fig. 119 Distribution of the African species of *Amphipsyche*.

coast (Fig. 119); this distribution coincides closely with the distribution of permanent waters in Africa (Gourou, 1970). The species is often caught in very large numbers, especially at light.

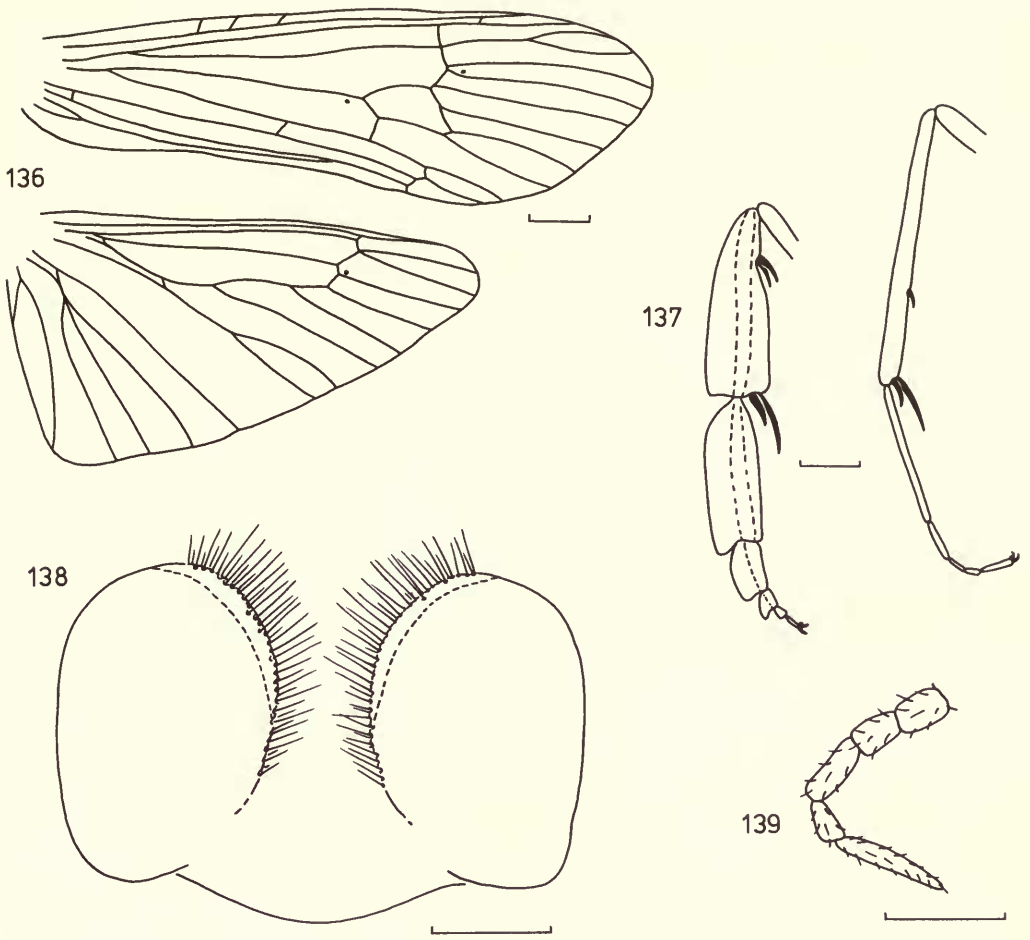
The synonymy of *curvinerve* with *senegalensis* was suspected by Kimmins (1962); the only remaining syntype of *curvinerve*, from the Alfieri collection, now in the USNM, has genitalia indistinguishable from those of typical *senegalensis*. Ulmer (1963) retained the name *curvinerve* when describing the larva of this species, but he admitted that he could not separate the two species. Ulmer had seen no females from West Africa to compare with his Egyptian examples, and he rightly suspected that his Sudanese specimens represented a different species: this was described as *ulmeri* by Kimmins (1962).

The female figured by Savigny (1813) from Egypt is certainly this species, though not named; this was the first published figure of a species of *Amphipsyche*.

The larva of *senegalensis* was described by Hickin (1955), Jacquemart (1957), Marlier (1962)



Figs 120–125 *Amphipsyche senegalensis* ♂. 120, wing venation; 121, mid and hind legs; 122, maxillary palp; 123, genitalia, lateral view; 124, phallotheca, lateral view; 125, genitalia, dorsal view.



Figs 136–139 *Amphipsyche pellucida* ♀. 136, wing venation; 137, mid and hind legs; 138, eighth sternites; 139, maxillary palp.

Remarks. Although this species clearly belongs in the 'African' section of the *meridiana*-group, it has no close affinities with any other species. It is the only species found in Madagascar, and morphologically the form of the phallotheca renders it easily identifiable. This is the first time that the male has been described.

Navás (1923) mis-read the type-locality of *pellucida* as 'Maeratanana'; this also applies to other species described in the same paper.

Material examined

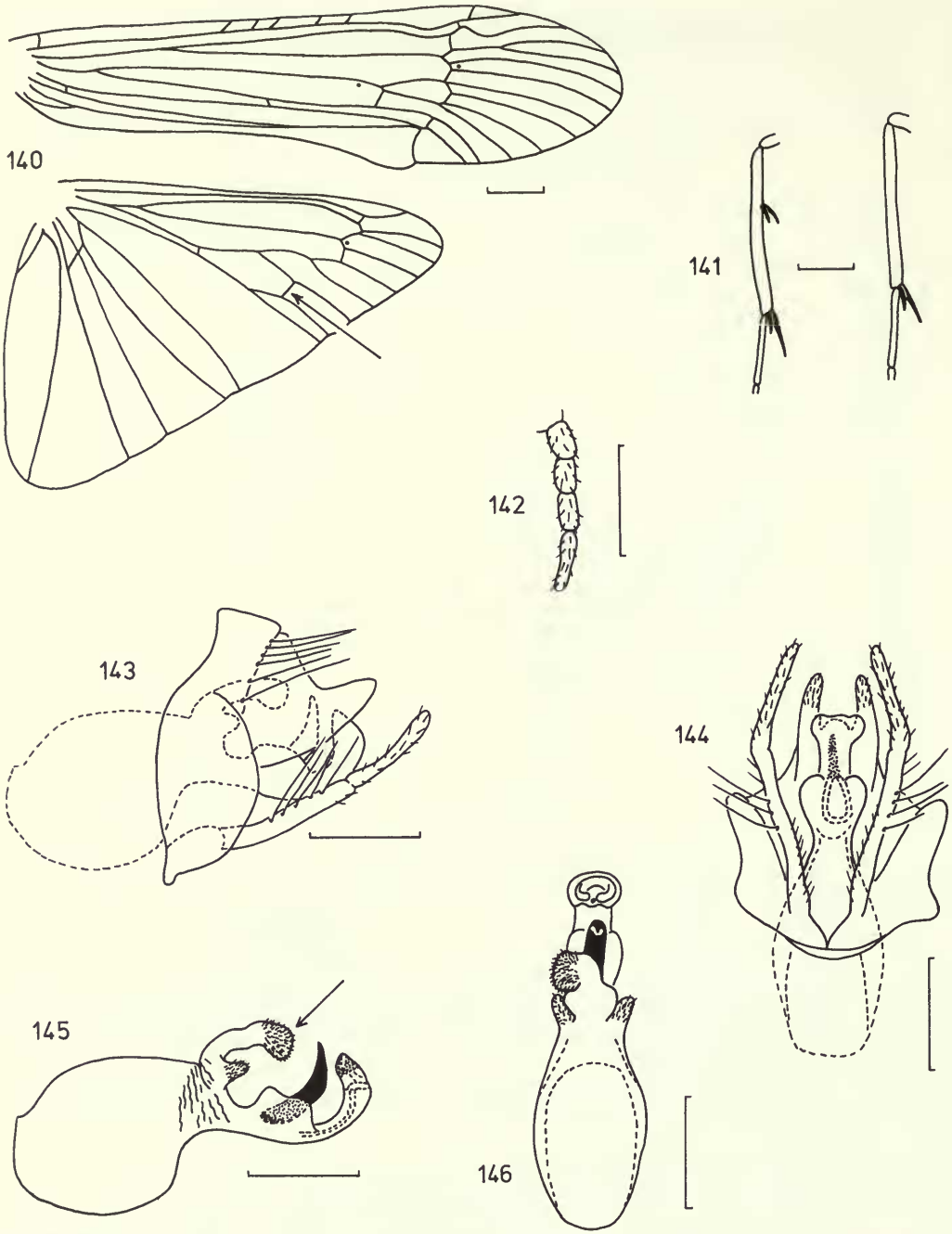
Holotype ♀, **Madagascar**: Maevatanana [no further data] (MNHN).
3 ♂, 13 ♀. **Madagascar** (BMNH, USNM).

Amphipsyche instabilis Kimmins

(Figs 140–150; distribution, Fig. 119)

Amphipsyche instabilis Kimmins, 1963: 126. Holotype ♂, Ethiopia (BMNH) [examined].
Phanostoma plicata Jacquemart, 1963: 363. LECTOTYPE ♂, Zimbabwe (ZI), here designated [examined]. **Syn. n.**

♂. Antenna up to 33 mm, with *c.* 90 segments. Fore wing 11–14 mm. Body pale yellowish brown, antennal



Figs 140–146 *Amphipsyche instabilis* ♂. 140, wing venation; 141, mid and hind tibiae; 142, maxillary palp; 143, genitalia, lateral view; 144, genitalia, ventral view; 145, phallotheca, lateral view; 146, phallotheca, dorsal view.

segments becoming gradually more fuscous towards apex, narrowly annulated with brown. Fore wing pale yellow with no markings; venation as in Fig. 140; cross-vein present between M_{3+4} and Cu_{1a} in hind wing. Apical venation often irregular in both fore and hind wings. Spurs 0.4.2 (Fig. 141). Maxillary palp 4-segmented, apical segment short and not secondarily annulated (Fig. 142).

♀ (allotype only). Antennal length unknown (specimen damaged). Fore wing 9 mm. Coloration as in ♂, venation as in Fig. 147; cross-vein between M_{3+4} and Cu_{1a} in hind wing as in ♂. Spurs 0.2.2 (Fig. 148). Maxillary palp 4-segmented (Fig. 149), similar to that of ♂.

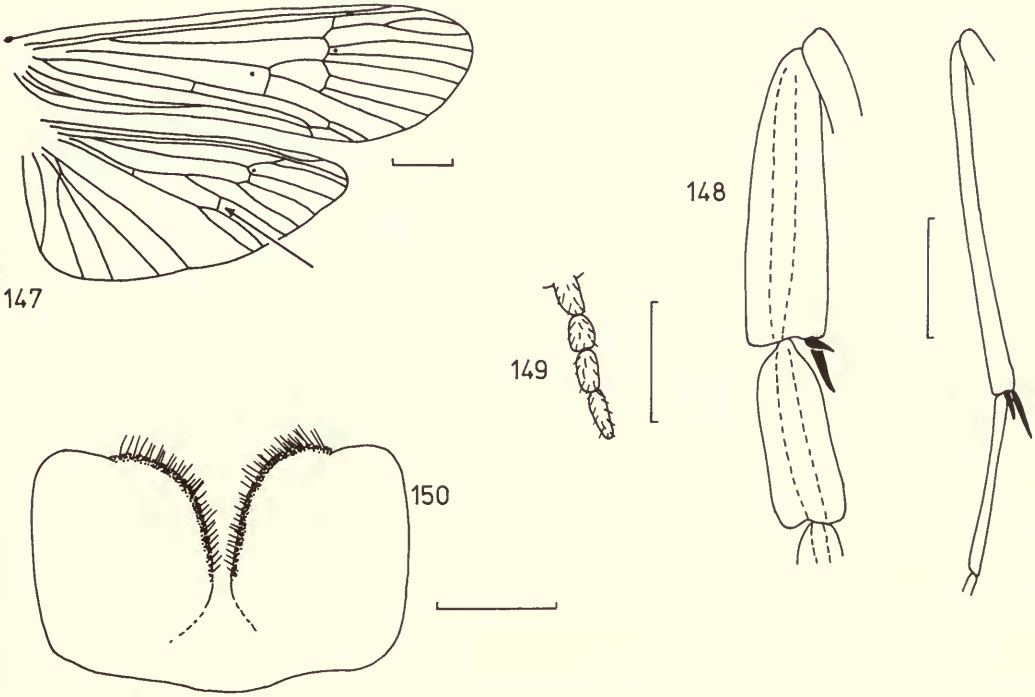
GENITALIA ♂ (Figs 143–146). Ninth segment only moderately broad laterally. Base of phallotheca very large and rounded, stem short and greatly thickened; dorsal clavate process present, with curved stem, apex covered with fine spines (Fig. 145); on either side of process a similarly spinose triangular lobe. Mid endothecal spines fused to form single median spine, very thick and curved dorsally. Lower apex of phallotheca elongate, curved dorsally, extreme apex globular. Inferior appendage narrow, slightly sinuate; terminal segment moderately well differentiated.

GENITALIA ♀ (Fig. 150). Eighth sternites broad and squarish, with rounded indentation in posterior edge; inner thickened edges narrow.

REMARKS. Although this species is closely related to the other African species of the genus, it is easily recognized. Externally, both sexes are easily identified by the extra cross-vein between M_{3+4} and Cu_{1a} in the hind wing which is unique amongst the African species, though paralleled in *proluta*, the type-species of the genus. The male genitalia are highly distinctive; the elongate dorsal process and single median endothecal spine are not found in any other species. The only known female closely resembles the female of *senegalensis*, which is found in the same locality, but apart from the venational character already mentioned, it can easily be distinguished by the 4-segmented maxillary palp and the squarish eighth sternites.

The specimen here designated as lectotype of *plicata* was labelled 'type' by Jacquemart, and the paralectotypes as 'paratypes', but these designations were not pubished.

Although the descriptions of *instabilis* and *plicata* were published in the same year, there is no doubt that Kimmins's appeared first. His paper was officially published on 20th February 1963 and, according to data in the BMNH Entomology Department Library, it was definitely available before the end of that month. The book in which Jacquemart's paper appeared has no exact date of publication, but the copy in the BMNH Zoology Department Library was received



Figs 147–150 *Amphipsyche instabilis* ♀. 147, wing venation; 148, mid and hind tibiae; 149, maxillary palp; 150, eighth sternites.

on 11th October 1963. Further enquiries to the ZI revealed that their copy was received on 25th November 1963 (Tjeder, *in litt.*), and the copy in the Kungliga Biblioteket, Stockholm (the Swedish copyright library) was not received until February 27th 1964 (Lilliestam, *in litt*). It seems certain, therefore, that the description of *plicata* was not published until at least October 1963, and that the name *instabilis* has priority.

MATERIAL EXAMINED

Holotype ♂ of *instabilis*, **Ethiopia**: Dawa River, 12 km N. of Hudat, 12.iv.1961 (*Tjønneland*) (slide preparation, BMNH). Lectotype ♂ of *plicata*, **Zimbabwe**: Victoria Falls, 16.v.1951 (slide preparation, ZI).

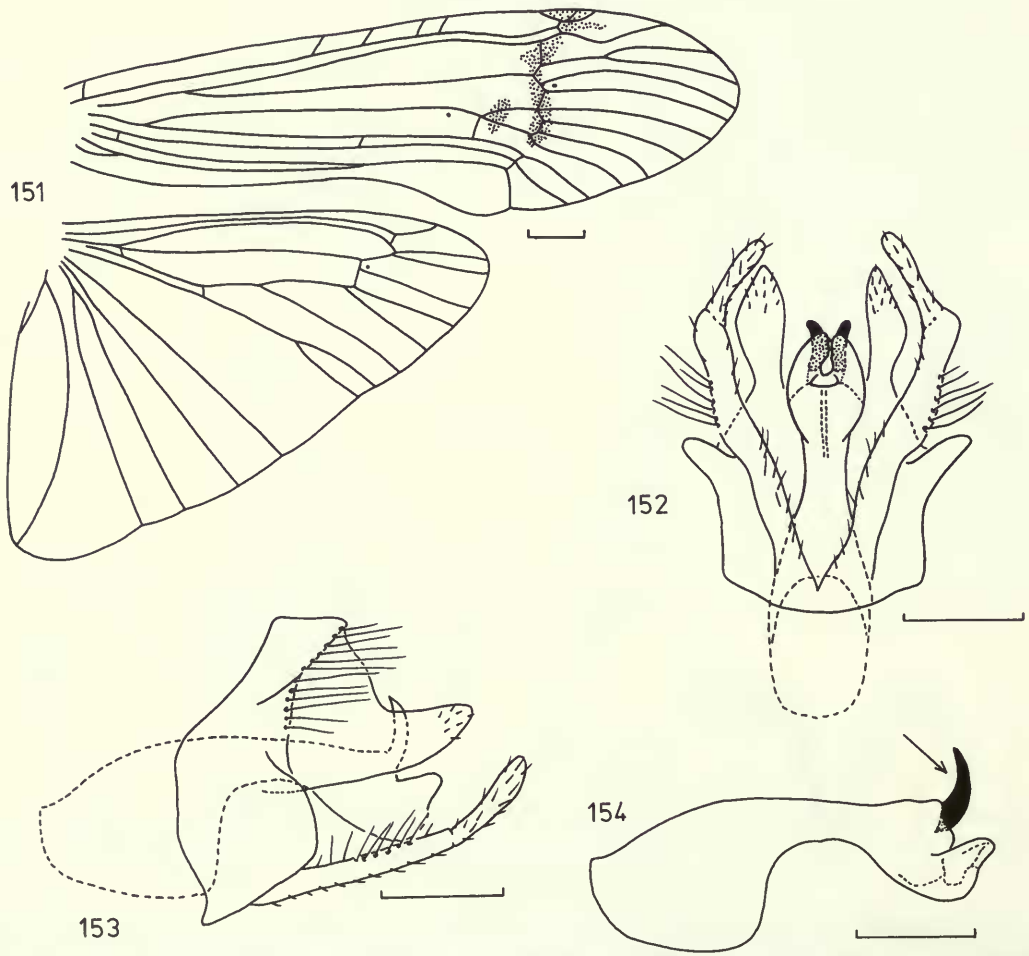
38 ♂, 1 ♀, **Ethiopia** (18 ♂ paratypes of *instabilis* and 1 ♀ allotype inadvertently labelled as '♂ paratype' by Kimmins), **Zimbabwe** (5 ♂ paralectotypes of *plicata*), **Zambia** (BMNH, IRSNB, USNM, ZI).

Amphipsyche ulmeri Kimmins

(Figs 151–154; distribution, Fig. 119)

[*Phanostoma senegalense* Brauer; Ulmer, 1923: 19 (*partim* – specimens from Sennar only); 1924: 2. Misidentifications.]

Amphipsyche ulmeri Kimmins, 1962: 89. Holotype ♂, SUDAN (NM) [examined].



Figs 151–154 *Amphipsyche ulmeri* ♂. 151, wing venation; 152, genitalia, ventral view; 153, genitalia, lateral view; 154, phallotheca, lateral view.

♂ (holotype only). Antenna 32 mm, with *c.* 70 segments. Fore wing 14 mm. Antennal segments pale golden brown, annulated with dark brown. Head, thorax and abdomen yellowish brown. Fore wing pale yellow with indistinct brownish shading across anastomosis; venation as in Fig. 151. Spurs 0.4.2. Maxillary palp as in *senegalensis* (*cf.* Fig. 122).

♀. No specimens seen, but see 'Remarks' below.

GENITALIA ♂ (Figs 152–154). Lateral part of ninth segment broad and squarish. Base of phallotheca broad, extreme apex bluntly pointed; mid endothecal spines long and stout, curved abruptly dorsally (Fig. 154). Inferior appendage strongly sinuous in ventral view, terminal segment moderately well differentiated.

REMARKS. *A. ulmeri* and *scottae* are closely related, despite their widely separate distributions (Fig. 119), both species having very similar male genitalia. However, *ulmeri* can be distinguished by the sharply up-turned mid endothecal spines.

Kimmins (1962) mentioned the existence of females from the type-locality, Sennar, in Ulmer's collection. Subsequently Ulmer (1963) described these females as being distinguishable from Egyptian females of *curvinerve* (= *senegalensis*) by the less sinuous *Rs* in the fore wing and the spur formula of 0.3.2. It is quite probable that these are females of *ulmeri*, but the spur formula is not significant, as Kimmins (1963) showed that there is great variation in the spurs of female *senegalensis*, 0.3.2 occurring in that species also.

MATERIAL EXAMINED

Holotype ♂, **Sudan**: Sennar, 18–27.ii.1914 (*Ebner*) (NM).

Amphipsyche scottae Kimmins

(Figs 155–164; distribution, Fig. 119)

Amphipsyche scottae Kimmins, 1962: 93. Holotype ♂, SOUTH AFRICA (BMNH) [examined].

♂. Antenna *c.* 45 mm, with *c.* 95 segments. Fore wing 16–19 mm. Body yellowish brown, antenna narrowly annulated with brown, segments becoming more fuscous towards apex. Fore wing pale yellow, with slightly darker area along costa and near Sc–R_1 cross-vein, often indistinct. Venation as in Fig. 155. Spurs 0.4.2 (Fig. 156). Maxillary palp 5-segmented, 5th segment approximately equal in length to segments 1 and 2 combined, not secondarily annulated (Fig. 157).

♀. Antenna *c.* 20 mm, with *c.* 70 segments. Fore wing 14–15 mm. General coloration as in ♂; fore wing with no darker markings. Venation as in Fig. 161. Spurs 0.4.2 (Fig. 162). Maxillary palp similar to that of ♂, but 5th segment shorter (Fig. 164).

GENITALIA ♂ (Figs 158–160). Ninth segment broadly rounded laterally. Base of phallotheca broadly triangular, with pronounced corner on dorsal side. Ventral apex forming pair of rounded lobes; extreme apex bluntly pointed (Fig. 159). Mid endothecal spines long, curved dorsally. Inferior appendage slender, terminal segment moderately well differentiated.

GENITALIA ♀ (Fig. 163). Eighth sternites broad and squarish, with slight indentation in middle of posterior edge. Inner thickened margin extending far towards anterior edge.

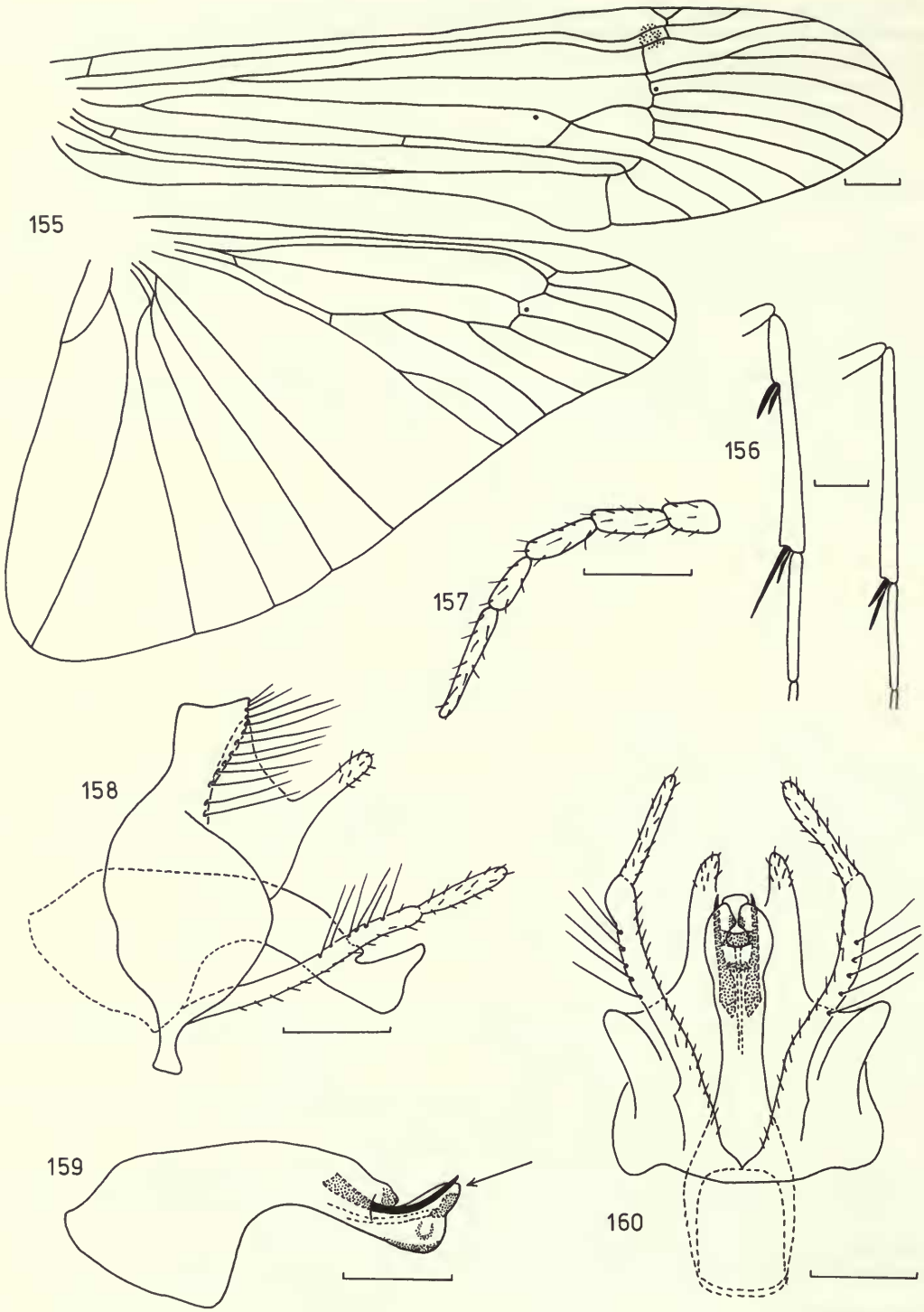
REMARKS. *A. scottae* most closely resembles *ulmeri* in that the males of both species have the tip of the phallotheca bluntly pointed in lateral view, but *scottae* can be distinguished by the gently curved mid endothecal spines, which are sharply up-turned in *ulmeri*.

The larva of this species was described by Scott (in press), and some aspects of its biology are mentioned by Chutter (1963; 1968); see p. 79.

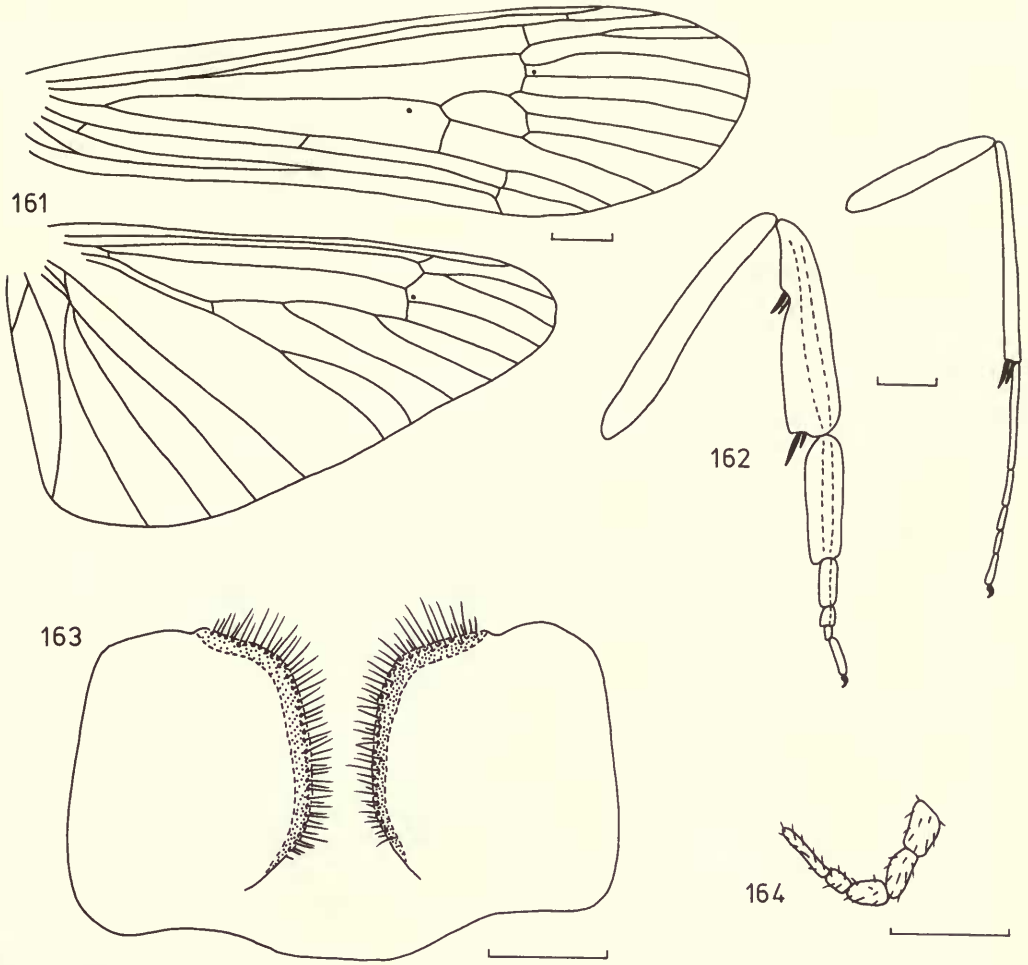
MATERIAL EXAMINED

Holotype ♂, **South Africa**: Natal, Wilge R., 5 miles [8 km] below Harrismith, 10.ii.1959 (slide preparation, BMNH).

12 ♂, 2 ♀, **South Africa** (12 ♂, 1 ♀ paratypes) (BMNH).



Figs 155–160 *Amphipsyche scottae* ♂. 155, wing venation; 156, mid and hind tibiae; 157, maxillary palp; 158, genitalia, lateral view; 159, phallotheca, lateral view; 160, genitalia, ventral view.



Figs 161–164 *Amphipsyche scottae* ♀. 161, wing venation; 162, mid and hind legs; 163, eighth sternites; 164, maxillary palp.

Amphipsyche fuscata Kimmins

(Figs 165–170; distribution, Fig. 119)

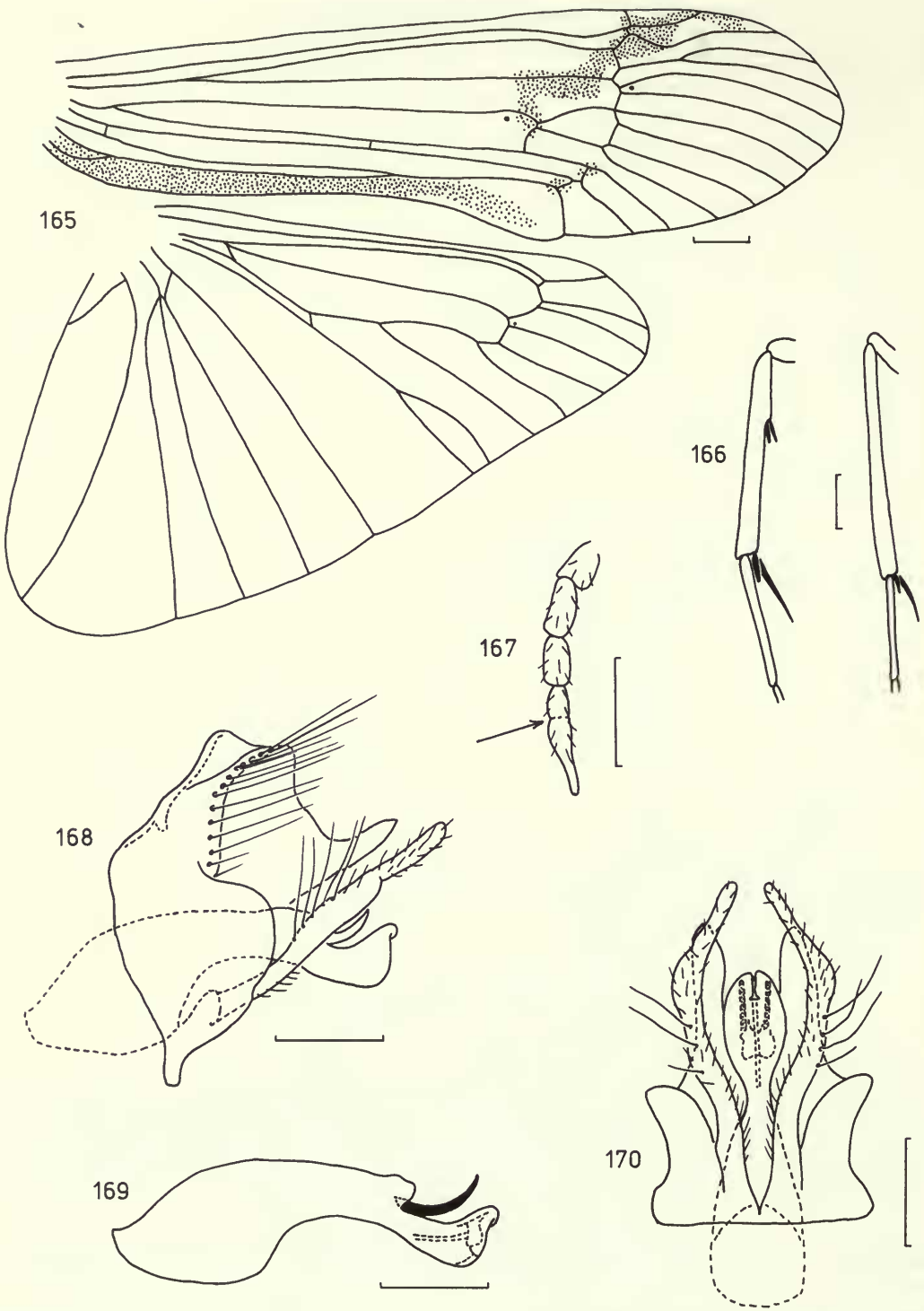
Amphipsyche fuscata Kimmins, 1963: 128. Holotype ♂, Ethiopia (BMNH) [examined].

♂. Antenna up to 35 mm, with *c.* 85 segments. Fore wing 12–17 mm. Body pale yellowish brown; basal 12–15 segments of antenna yellowish brown, remainder of flagellum fuscous. Fore wing pale yellow, with fuscous streak running obliquely from costal margin proximal to anastomosis; hind margin fuscous (these markings may be very faint). Venation as in Fig. 165. Spurs 0.4.2 (Fig. 166). Maxillary palp short, 4th and 5th segments imperfectly separated, 5th segment narrow apically, not secondarily annulated (Fig. 167).

♀. Unknown.

Genitalia ♂ (Figs 168–170). Lateral lobe of ninth segment somewhat squarish. Base of phallotheca narrow and rounded, apex elongate, produced into a bifid lobe. Mid endothecal spines long, curved upwards.

Remarks. Well-marked specimens of this species can be recognized by the oblique wing-marking, but identification of specimens with faint markings depends on the male genitalia, and here the close similarity with several other African species is apparent. However, *fuscata* differs



Figs 165–170 *Amphipsyche fuscata* ♂. 165, wing venation; 166, mid and hind tibiae; 167, maxillary palp; 168, genitalia, lateral view; 169, phallotheca, lateral view; 170, genitalia, ventral view.

from *scottae* and *ulmeri* in having the apex of the phallotheca rounded, not pointed, and from *berneri* and *corbeti* in having a narrow base to the phallotheca. *A. fuscata* is further distinguished by the unique maxillary palps, with the 4th and 5th segments only partly fused. Kimmins (1963) noted the colour of the palps, but did not notice their unusal form.

MATERIAL EXAMINED

Holotype ♂, **Ethiopia**: Koka Dam, 29.iii.1964 (*Tjønneland*) (slide preparation, BMNH).
62 ♂, **Ethiopia** (60 ♂ paratypes), **Sudan** (BMNH).

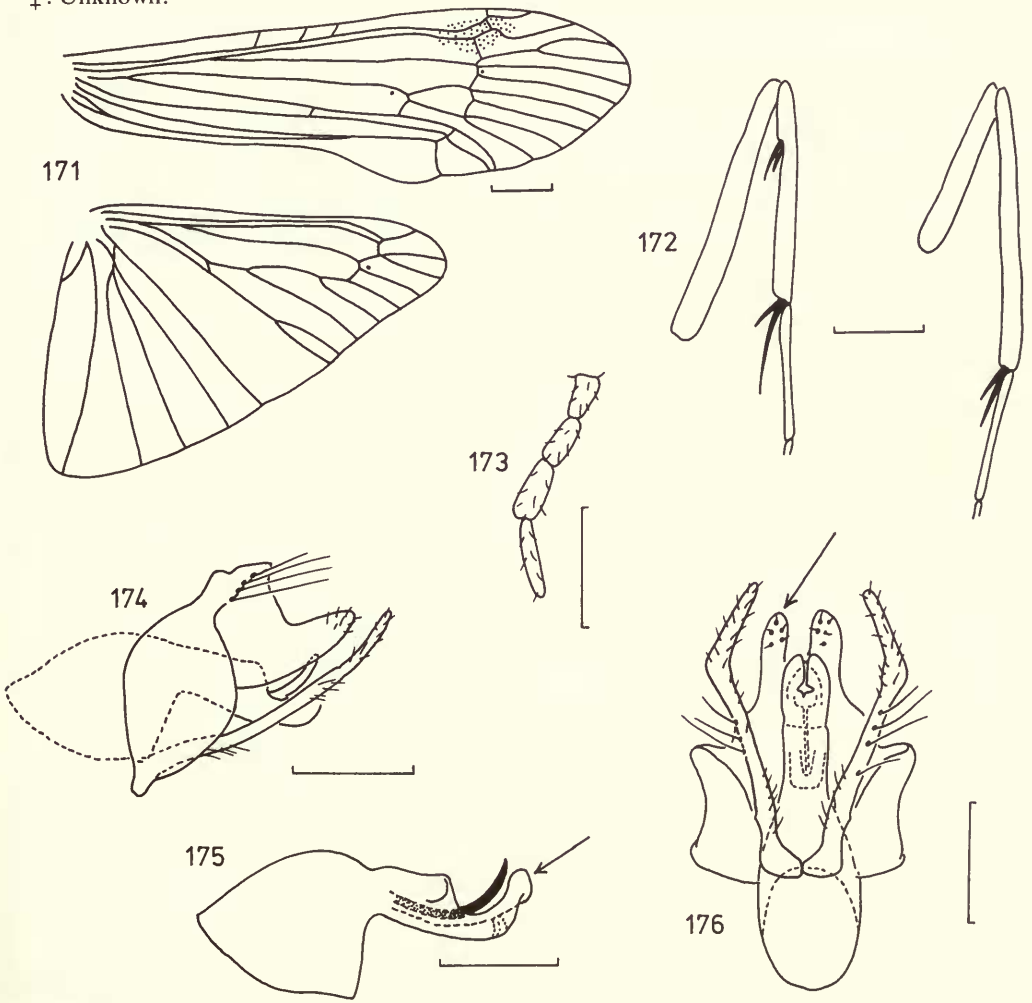
Amphipsyche corbeti Kimmins

(Figs 171–176; distribution, Fig. 119)

Amphipsyche corbeti Kimmins, 1962: 89. Holotype ♂, UGANDA (BMNH) [examined].

♂. Antenna up to 30 mm, with *c.* 85 segments. Fore wing 11–12 mm. Body pale yellowish brown, thorax pale brown dorsally, antenna pale greyish brown. Fore wing pale yellowish brown, usually with pale brown shading around R_1–*Rs* cross-vein. Venation as in Fig. 171. Spurs 0.4.2 (Fig. 172). Maxillary palp 4-segmented, terminal segment narrow and slightly elongate, but not secondarily annulated (Fig. 173).

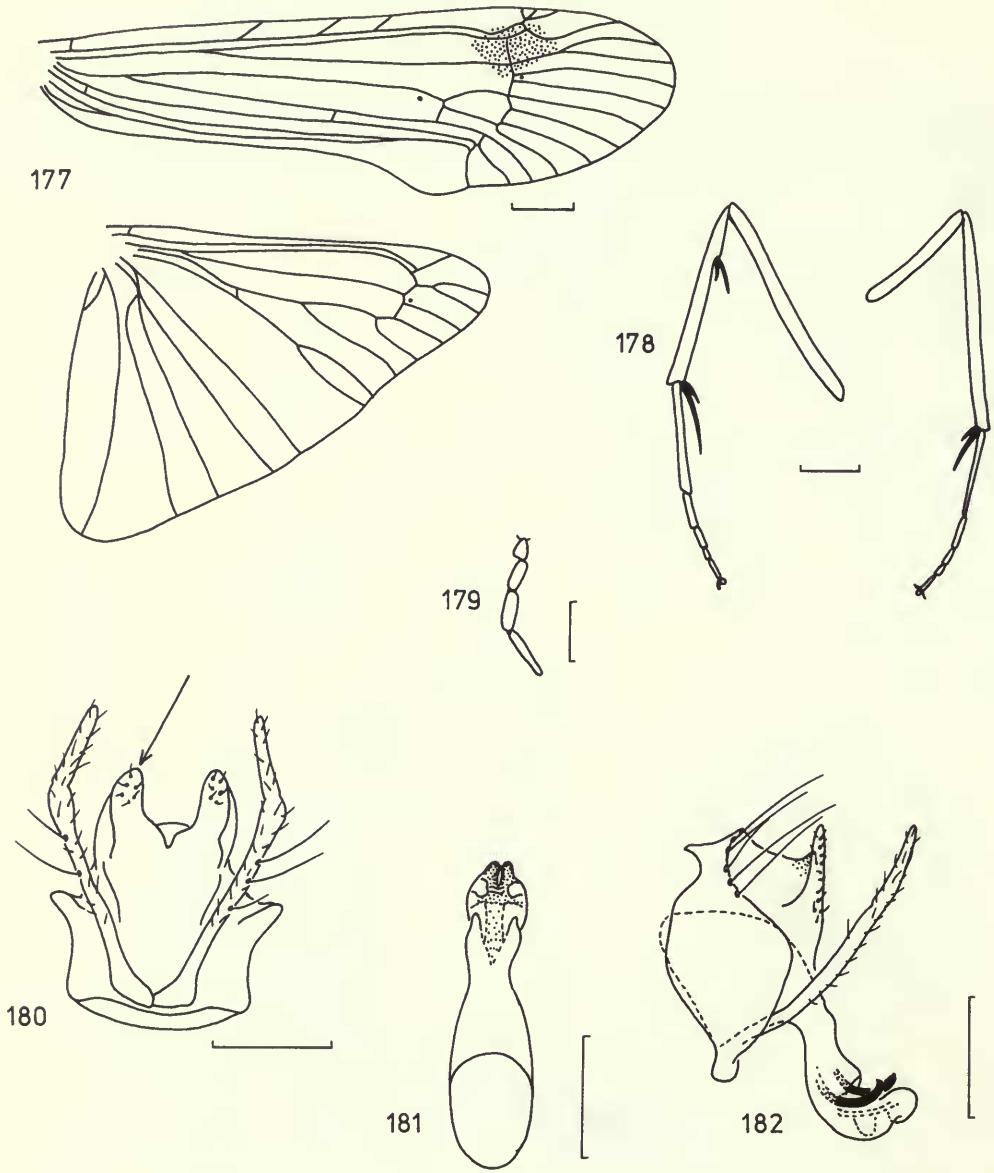
♀. Unknown.



Figs 171–176 *Amphipsyche corbeti* ♂. 171, wing venation; 172, mid and hind tibiae; 173, maxillary palp; 174, genitalia, lateral view; 175, phallotheca, lateral view; 176, genitalia, ventral view.

GENITALIA ♂ (Figs 174–176). Base of phallotheca broadly triangular, stem thickened, apex forming pair of lobes ventrally; mid endothecal spines long, curved dorsally. Inferior appendage slender, terminal segment scarcely differentiated.

REMARKS. This species closely resembles *berneri* and, to a lesser extent, *ulmeri*. It differs from *ulmeri* in the thicker stem of the phallotheca and the longer endothecal spines, and from *berneri* in the lobes of the tenth segment. These lobes are narrower in dorsal view in *corbeti*, and do not diverge. There are also slight differences in the apex of the phallotheca, best seen in ventral view.



Figs 177–182 *Amphipsyche berneri* ♂. 177, wing venation; 178, mid and hind legs; 179, maxillary palp; 180, genitalia, ventral view; 181, phallotheca, ventral view; 182, genitalia, lateral view.

MATERIAL EXAMINED

Holotype ♂, **Uganda**: Northern Province, Victoria Nile, Karuma Falls [no date] (*Corbet*) (slide preparation, BMNH).

33 ♂ paratypes, **Uganda** (BMNH).

Amphipsyche berneri Kimmins

(Figs 177–182; distribution, Fig. 119)

[*Phanostoma senegalense* Brauer; Kimmins, 1957*a*: 13 (*partim* – specimens from Gold Coast [Ghana] only). Misidentification.]

Amphipsyche berneri Kimmins, 1962: 91. Holotype ♂, GHANA (BMNH) [examined].

♂. Antenna *c.* 25 mm, with *c.* 85 segments. Fore wing 11–12 mm. Body coloration uncertain (both specimens originally preserved in alcohol). Fore wing yellowish brown, with darker marking centred on R_1–*Rs* cross-vein; venation as in Fig. 177. Spurs 0.4.2 (Fig. 178). Maxillary palp 4-segmented, terminal segment scarcely longer than 3rd (Fig. 179), not secondarily annulated.

♀. Unknown.

GENITALIA ♂ (Figs. 180–182). Base of phallotheca broadly triangular; ventral apex forming pair of lobes; mid endothecal spines long and curved dorsally. Inferior appendage slender, terminal segment not clearly differentiated.

REMARKS. This species is very similar to *corbeti*, both externally and in the form of the genitalia. It can be distinguished by slight differences in the shape of the apex of the phallotheca and by the lobes of the tenth segment. These are broader and more divergent in dorsal view in *berneri*, although it should be noted that in the paratype (figured here) the lobes are less divergent than in the holotype figured by Kimmins (1962: 91, fig. 26). The holotype is now mounted laterally as a permanent slide preparation.

Kimmins did not comment on the 4-segmented maxillary palps, although these are clearly visible in his slide preparation of the holotype.

MATERIAL EXAMINED

Holotype ♂, **Ghana**: Volta R., Senchi, 1.viii.1950 (*Berner*) (slide preparation, BMNH).

1 ♂ paratype, **Ghana** (BMNH).

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Synonyms are in *italics*; principal references are in **bold**. References to Table 1 (p. 82), the cladogram (p. 83) and the check-list (p. 85) are not included.